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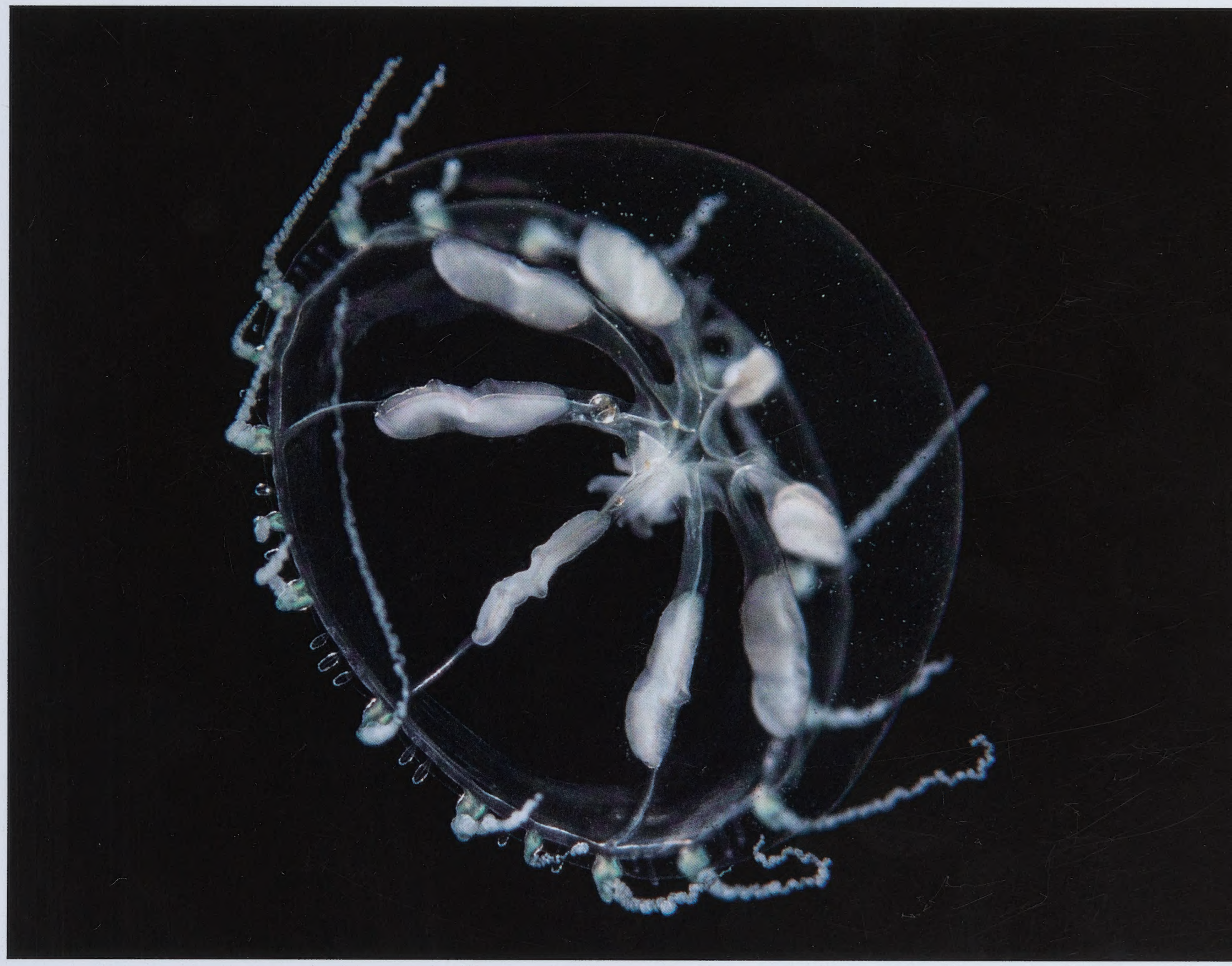

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A new species of *Prionoglaris* Enderlein (Psocodea: 'Psocoptera': Prionoglarididae) from an Armenian cave, with an account of the distribution of the genus

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Abstract: The cavernicolous species *Prionoglaris kapralovi* sp. nov. is described from Armenia. A key to the three species of *Prionoglaris* known from adults is given and the variability of some characters is discussed. All published locality records of the genus, including those of nymphs, are summarized, along with previously unpublished records based on the collection of the Geneva Natural History Museum.

Keywords: Insecta - Trogiomorpha - Morocco.

INTRODUCTION

The family Prionoglarididae, the members of which are predominantly cavernicolous, is one of the most fascinating families of psocids, due to its mix of partly archaic and partly extremely derived morphology and the specialized reproductive biology of some genera, e. g. the use of a female penis in the Neotropical genus *Neotrogla* Lienhard in Lienhard *et al*., 2010b (Yoshizawa *et al*., 2014; Lienhard, 2020). The family belongs to the suborder Trogiomorpha and is one of the most basal groups of the order Psocodea, probably having existed since the mid-Permian (Yoshizawa *et al*., 2006, 2019). The monophyly of the Prionoglarididae is still controversial (Yoshizawa *et al*., 2006; de Moya *et al*., 2021). However, according to Yoshizawa & Lienhard (2020) two morphological characters may be considered as synapomorphies of the members of this family: broadened and rounded forewings, and long slender antennae with a reduced number of segments (at most 13 flagellomeres). Both characters are unique within the suborder Trogiomorpha. Monophyly of the family is also supported by phylogenetic analyses based on mitochondrial genome sequences (Yoshizawa *et al*., 2017).

The family Prionoglarididae is subdivided in two subfamilies, Prionoglaridinae and Speleketorinae (Lienhard, 2004; Yoshizawa *et al*., 2018). The type genus is *Prionoglaris* Enderlein, 1909 which contains three species: *P. stygia* Enderlein, 1909 and *P. dactyloides* Lienhard, 1988, known from the western Palaearctic, and *P. lindbergi* Badonnel, 1962, only known from a single nymph collected in Afghanistan. The latter is not included in the key below because there are no diagnostic characters to distinguish nymphs at the species level within this genus. The species definitions are based on adult characters, especially on male genitalia. Unfortunately, adults of this genus are rarely collected, usually most of the specimens collected in caves are nymphs (Lienhard, 1988). However, nymphs can easily be recognized as belonging to the genus *Prionoglaris* (see diagnosis in Lienhard, 1988, 1998 and habitus figure in Schneider & Weber, 2013), nymphal records therefore provide valuable data on the geographic distribution of the genus.

In the following a new species of *Prionoglaris* is described on the basis of a male and a female from an Armenian cave. The assignment of a Moroccan population to the species *Prionoglaris stygia* is discussed and some information on the variability of several morphological characters is provided. A species key to adults is given and the known distribution of the genus is summarized, including also records of nymphs.

MATERIAL AND METHODS

The type material of the new species, and of *P. dactyloides* and *P. lindbergi,* as well as the specimens examined for unpublished records are deposited in the Muséum d'histoire naturelle, Geneva, Switzerland (MHNG). The type material of *P. stygia* (only nymphs, syntypes) was not examined because it could not be located (see Lienhard, 1988: 95). Dissection and slide-mounting was performed according to the methods described by Lienhard (1998). Abbreviations used in the description: AP = areola postica

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(marginal cell in forewing formed by veins CuA1 and CuA2); BL = body length (in alcohol); FW = forewing (length); FWw = forewing (greatest width); HW = hindwing (length); IO/D = shortest distance between compound eyes divided by longitudinal diameter of compound eye in dorsal view of head. Abbreviations of wing veins are used according to Yoshizawa (2005).

TAXONOMIC PART

Prionoglaris Enderlein, 1909

Synonymy: see Lienhard & Smithers, 2002.

Type species: *Prionoglaris stygia* Enderlein, 1909.

Generic diagnosis: See Lienhard (1988, 1998).

Diagnoses of known species: For *P. stygia* see Lienhard (1988, 1998) and additional figures in Lienhard (2004, 2011); for *P. dactyloides* see Lienhard (1988, 1998); for *P. lindbergi* see Badonnel (1962, nymph only).

Prionoglaris kapralovi sp. nov.

Figs 1-2

Holotype: MHNG; male (some parts slide-mounted); Armenia, 8.3 km SW of Yeghegnadzor, Mozrov Cave; WGS84 39.71258, 45.25953; 1540 m a.s.l., under stones near cave entrance; 14.AUG.2018; leg. S. A. Kapralov.

Paratype: MHNG; female (some parts slide-mounted); same data as for holotype.

Diagnosis: This new species can be distinguished from all known species of the genus *Prionoglaris* by the absence of an internal membranous vesicle on the anterior claw and by the absence of a basal tooth on the posterior claw of each pretarsus (Fig. 2C-D). See also key below.

Etymology: The species is dedicated to Sergei A. Kapralov who collected the type material.

Description

General characters: Head and thorax (including antenna, maxillary palp and legs) yellowish to light or medium brown. Vertex, frons and genae with some small brown patches. Compound eye uniformly dark grey to black (after 2 years in alcohol). Wings hyaline, veins medium brown, pterostigma colourless but slightly opaque (Fig. 1B). Abdomen whitish, dorsally and laterally with numerous patches of dark hypodermal pigment forming irregular transversal bands (Fig. 1A-B). Terminalia light to medium brown, ventro-median process of phallosome dark brown (Fig. 1C).

Mouthparts typical for the genus; lacinial rudiment with an acuminate tip (Fig. 2E). Antennae long and slender (Fig. 1A), both damaged in male and female examined (highest number of flagellomeres observed is 7, in right antenna of holotype, 7th flagellomere broken near base). Anterior claw of each pretarsus (Fig. 2C) with a long basal seta, lacking internal membranous vesicle and preapical denticle. Posterior claw of each pretarsus simple (Fig. 2D), lacking basal tooth and preapical denticle. Forewing broadly rounded, clearly longer than twice its width (FW/FWw about 2.4); venation typical for the genus (Fig. 2A), but AP somewhat shorter in male than in female (in male its marginal length about same as its height, see Fig. 1A; in female marginal length slightly exceeding height, see Fig. 2A-B). Hindwing as in *P. stygia*. Vein aberrations observed in forewings and hindwings: right forewing of female with a cross-vein between R1 and R2+3, and M1 bifurcate near wing margin (Fig. 2B); right forewing of male with a short spurvein on R1, just basally to point where Sc reaches R1 (Fig. 1A); left hindwing of male with a transversal vein between R1 and Rs (Fig. 1A), and both hindwings of female with slightly aberrant M2.

Male genitalia: Sac-like proximal body of phallosome relatively short (Fig. 2H-I), about half of total length of phallosome; ventro-median process strongly curved in lateral view (Fig. 2H); dorso-lateral appendages of

Key to species of the genus *Prionoglaris* (adults only)

Note: Adults of *P. lindbergi* are not known (see Introduction).

1A Claws of each pretarsus clearly asymmetrical. Anterior claw with a long basal seta and an internal membranous vesicle situated in basal half of claw (Fig. 3B). Posterior claw simple but bearing a short basal tooth (Fig. 3C), preapical denticle usually absent, rarely present (Fig. 3C), sometimes minute. Sac-like proximal part of phallosome longer than half of total length of phallosome (Fig. 3A). Spermapore sclerite a thin and weakly sclerotized plate, spermathecal duct running straight through the sclerite (Fig. 3K-L) 2

1B Asymmetry of pretarsal claws less pronounced. Anterior claw with a long basal seta but lacking internal membranous vesicle (Fig. 2C). Posterior claw simple, lacking basal tooth and preapical denticle (Fig. 2D). Sac-like proximal part of phallosome relatively short (Fig. 2H-I), about half of total length of phallosome. Spermapore sclerite a thick and heavily sclerotized plate, spermathecal duct within the sclerite curved (Fig. 2F-G) ..... *P. kapralovi* sp. nov.

2A Dorso-lateral appendages of phallosome of about same width between base and broadly rounded apex (Fig. 3I) or only weakly narrowing towards apex (Fig. 3E-H) ..... *P. stygia*

2B Dorso-lateral appendages of phallosome digitiform, narrow throughout except for slightly broader basal one third (Fig. 3J)..... *P. dactyloides*

about same width between base and apex, only weakly narrowing towards apex (Fig. 2I); medio-internal appendage with one fine hair on each side (Fig. 2H-I).
Female genitalia: Subgenital plate and gonapophyses typical for the genus, only external valvula well developed, bearing 6 apically hooked setae near broadly rounded apex. Spermapore sclerite a thick and heavily sclerotized plate, proximally broadly rounded, distally narrowly rounded (Fig. 2F); spermathecal duct curved inside the sclerite (Fig. 2G) and widened towards spermathecal vesicle shortly after the spermapore sclerite (length of the narrow portion of the duct, before widening, about 1.5 times length of spermapore sclerite).

Measurements: *Male*: BL = 3.3 mm; FW = 3.7 mm; FWw = 1.5 mm; HW = 2.5 mm; IO/D = 1.8. – *Female*: BL = 4.1 mm; FW = 4.1 mm; FWw = 1.7 mm; HW = 2.7 mm; IO/D = 1.9.

Distribution: Only known from type locality in Armenia.

Type locality: Armenia, Mozrov Cave near Yeghegnadzor, 1540 m a.s.l. This cave is situated on the

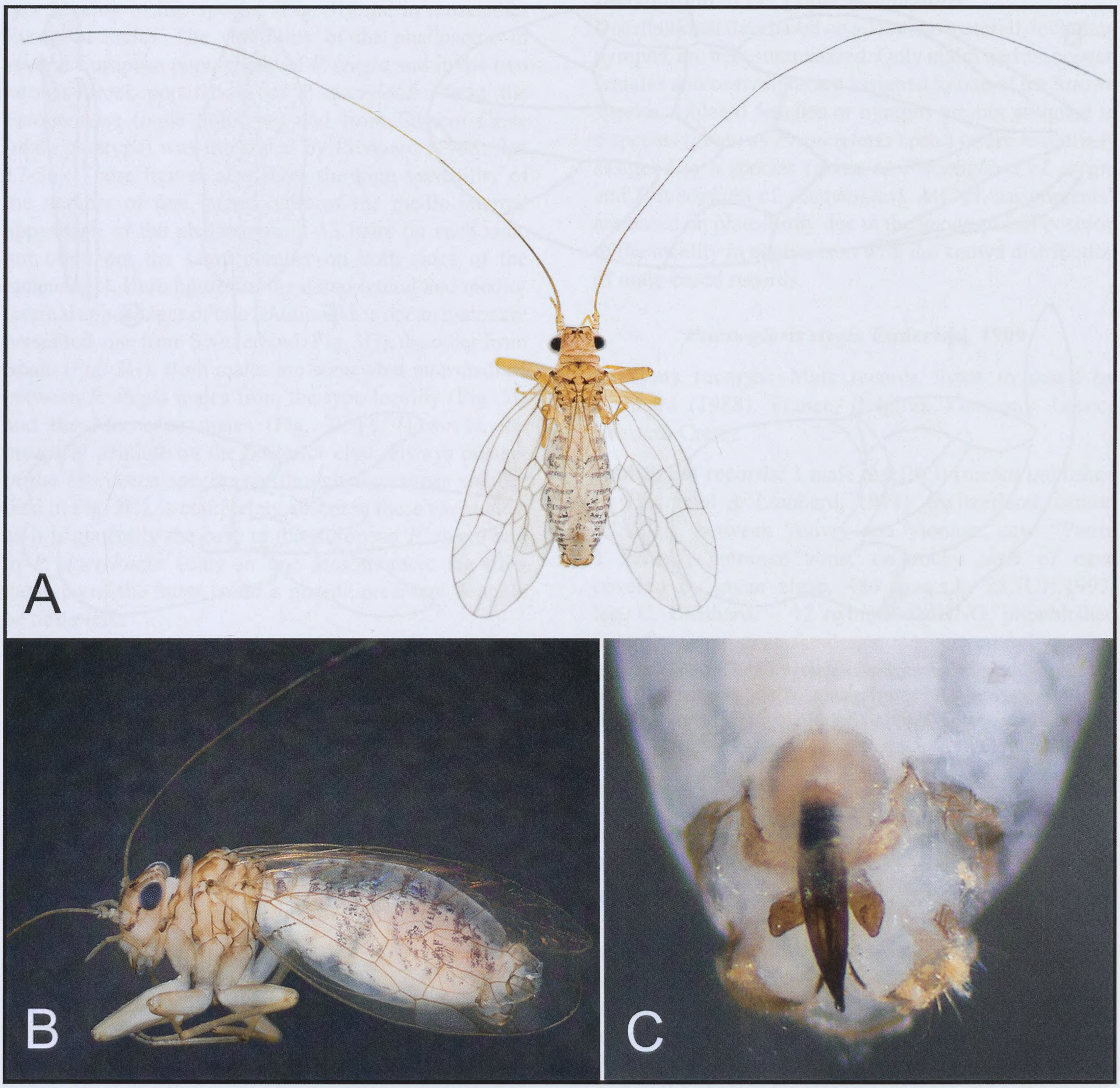

Fig. 1. *Prionoglaris kapralovi* sp. nov. (A) Habitus of male, dorsal view of holotype, in alcohol (body length 3.3 mm). (B) Habitus of female, lateral view of paratype, in alcohol (body length 4.1 mm). (C) Male terminalia, ventral view of holotype, in alcohol. Photographs by S. A. Kapralov.

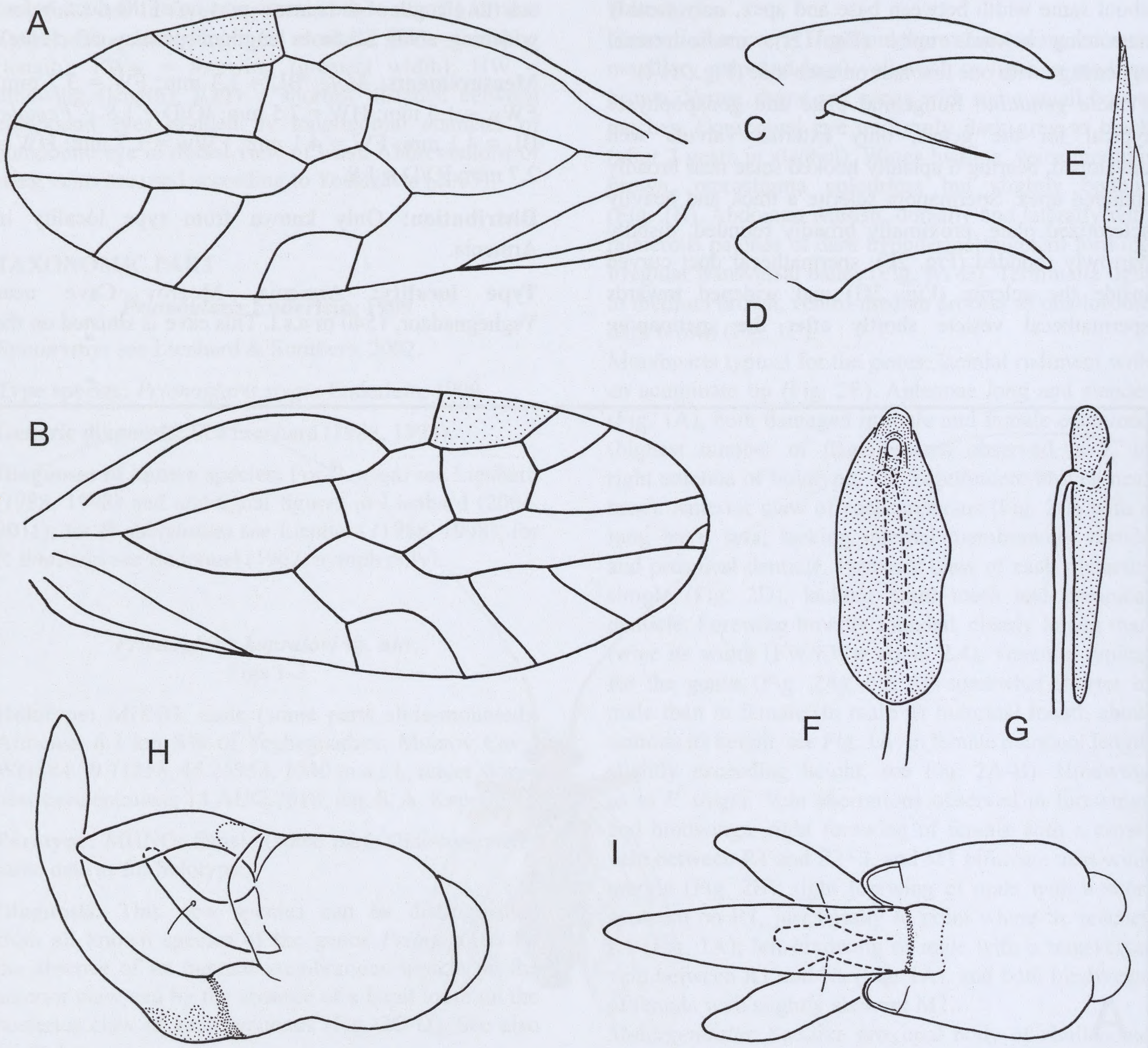

Fig. 2. *Prionoglaris kapralovi* sp. nov., female (A-G), male (H-I). (A) Left forewing. (B) Right forewing. (C) Anterior claw of hind pretarsus. (D) Posterior claw of hind pretarsus. (E) Lacinial rudiment (length 0.2 mm). (F) Spermapore sclerite and distal part of spermathecal duct, ventral view. (G) Idem, optical longitudinal section, lateral view. (H) Phallosome, lateral view. (I) Idem, ventral view.

rolling steppe-like plateau on the left bank of the Arpi river.

Remarks: Judging from most morphological characters, especially the male genitalia, this species clearly belongs to the genus *Prionoglaris*. However, the asymmetry of the claws of each pretarsus is less pronounced in the new species than in the other species of this genus, especially due to the absence of the membranous vesicle on the anterior claw. This membranous extension is always well developed in the other species of *Prionoglaris*. The presence of a membranous extension on the anterior claw has been considered as an autapomorphy of the subfamily Prionoglaridinae (Lienhard, 2004). No intra-generic variability concerning this character has previously been observed in this subfamily. The membranous extension is particularly well developed in the Oriental genus *Siamoglaris* Lienhard, 2004, and in the fossil genus *Palaeosiamoglaris* Azar, Huang & Nel in Azar *et al.*, 2017 from Burmese amber, but weakly developed in the fourth genus of this subfamily, the troglobitic *Speleopsocus* Lienhard in Lienhard *et al.*, 2010a which is only known from a single Venezuelan cave. Therefore the absence of this structure in the new species has to be interpreted as an apomorphic reduction. See the discussion below.

Remarks on a Moroccan sample of *Prionoglaris stygia*

The only morphological character that distinguishes the closely related species *P. stygia* and *P. dactyloides* is the shape of the dorso-lateral appendages of the phallosome. Specimens from a Moroccan sample assigned to *P. stygia*, collected in the Friouato Cave (see Distribution, below), slightly differ from European *P. stygia* by the shape of these appendages, and by the presence of a preapical denticle on the posterior claw of each pretarsus (Fig. 3C). The dorso-lateral appendages of the phallosome are apically slightly narrowing in the Morrocan males (Fig. 3E-F and Lienhard, 1996: figs 4-6, 1998: fig. 41b), while they are broadly rounded in *P. stygia* males from the type locality of this species (Fig. 3I) and in most other European males. The variability of the phallosome in several European populations of *P. stygia* and in the two known Greek populations of *P. dactyloides* from the Peloponnese (male holotype) and from Eastern Crete (male paratype) was illustrated by Lienhard (1988: figs 17-36). These figures also show the high variability of the number of fine lateral hairs of the medio-internal appendage of the phallosome (1-13 hairs on each side, but often not the same number on both sides of the appendage). Here figures of the dorso-lateral and medio-internal appendages of two additional European males are presented, one from Switzerland (Fig. 3G), the other from Spain (Fig. 3H). Both males are somewhat intermediate between *P. stygia* males from the type locality (Fig. 3I) and the Moroccan males (Fig. 3E-F). However, the preapical denticle on the posterior claw, always present in the Moroccan specimens (though sometimes smaller than in Fig. 3C), is completely absent in these two males, as it is generally the case in the European *P. stygia* and in *P. dactyloides* (only in one mesothoracic leg of a paratype of the latter could a minute preapical denticle be observed).

When looking for other potentially diagnostic characters which could allow the Moroccan specimens to be distinguished from the European *P. stygia*, I discovered some differences in the ratio between forewing length and width (FW/FWw) and in the micromorphology of the spermapore sclerite. In both sexes the Moroccan specimens have particularly broad and slightly shortened wings (Fig. 3D), with FW/FWw varying from 2.0 to 2.1 (N = 2). In the European *P. stygia* forewings are clearly longer than twice their width, FW/FWw varying from 2.2 to 2.5 (N = 6; the mean is 2.4). In *P. dactyloides* this ratio varies from 2.1 to 2.3 (N = 2).

In the only Moroccan female available for this study the spermapore sclerite is proximally broadly rounded and distally slightly elongated and beak-shaped (Fig. 3K). In the European *P. stygia* this sclerite is similar in shape to that of *P. kapralovi* sp. nov., i.e. narrowly rounded distally but not elongated and beak-shaped (see figures in Lienhard, 1988, 1998). However, in a female of *P. stygia* from the type locality (French Pyrenees) a distally weakly elongated spermapore sclerite was observed (Fig. 3M), about intermediate in shape between the other *P. stygia* and the Moroccan female.

In view of the considerable variability of the above mentioned characters, and of the low numbers of specimens examined for this study, the slight differences observed between the Moroccan population and the European *P. stygia* are not sufficient to warrant a formal separation of the Moroccan form as a new species. The only character which can be considered as diagnostic for the Moroccan form is the presence of a preapical denticle on the posterior claw of each pretarsus.

Distribution of the genus *Prionoglaris*

Distributional data based on all known material, including nymphs, are here summarized. Only males and associated females and/or nymphs are assigned to one of the known species. Isolated females or nymphs are not assigned to a species (given as *Prionoglaris* spec.) or are tentatively assigned to a species (given as *Prionoglaris* cf. *stygia* and *Prionoglaris* cf. *dactyloides*). All "cf.-assignments" are based on plausibility due to the geographical position of the locality in comparison with the known distribution of male-based records.

***Prionoglaris stygia* Enderlein, 1909**

Previous records: Male records listed in detail by Lienhard (1988): France, Belgium, Germany, Greece (western Crete).

Additional records: 1 male (MHNG) (record published by Badonnel & Lienhard, 1994); Switzerland, canton of Valais, between Vouvry and Vionnaz, cave "Pierre à Perret", entrance zone, on rocky wall of cave covered by green algae, 480 m a.s.l.; 28.JUN.1993; leg. C. Lienhard. – 12 nymphs (MHNG, unpublished record); same cave, under stones covered by green algae; 10.AUG.1989; leg. C. Lienhard. – 12 nymphs (MHNG, unpublished record); same data; leg. B. Hauser. – 1 nymph (MHNG, unpublished record); same data; leg. S. Hauser. – 2 nymphs (MHNG, unpublished record); same data, leg. P. Strinati. – 1 male, 1 female (MHNG, unpublished record); Spain, Prov. Castellon, W of Atzeneta del Maestrat, valley W of Eremita de Sant Juan, 485 m a.s.l., under stones in dense evergreen oak forest on steep, north facing slope; 30.MAY.2010; leg. S. Huber & A. Schönhofer. – Unspecified number of males (A. Baz, *in litt.* 1999; unpublished record); Spain, Madrid, Malaise trap and on *Quercus pyrenaica*. – 2 males, 6 females, 8 nymphs (recorded by Baz, 2003, without giving details where males were collected); Spain: three caves in Andalusia: Almeria, Sierra de Gador, cave "Cueva del Lobo", 800-900 m a.s.l.; Almeria, Sierra de Gador, cave "Cueva Nueva", 800-900 m a.s.l.; Jaen, Pontones, cave "Cueva del Jabali", 1400-1500 m a.s.l. – 3 males, 1 female

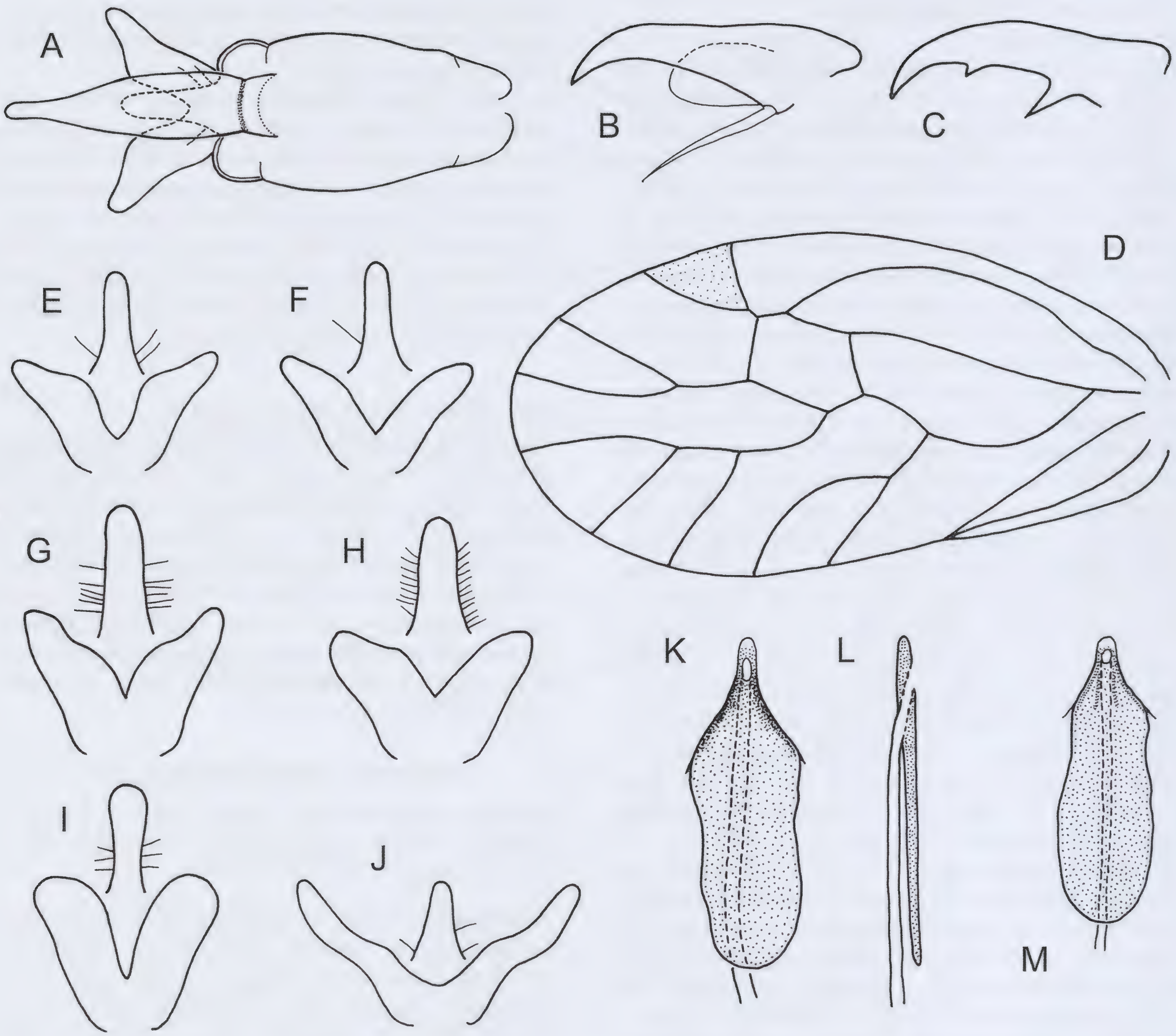

Fig. 3. *Prionoglaris* spp.: *P. stygia* males from Friouato Cave, Morocco (A-F), *P. stygia* male from Pierre à Perret Cave, Switzerland (G), *P. stygia* male from W of Atzeneta del Maestrat, Spain (H), *P. stygia* male from the type locality, Compagnaga Cave, French Pyrenees (I), *P. dactyloides*, male holotype (J), *P. stygia* female from Friouato Cave, Morocco (K-L), *P. stygia* female from the type locality, Compagnaga Cave, French Pyrenees (M). – (A) Phallosome, ventral view. (B) Anterior claw of hind pretarsus. (C) Posterior claw of hind pretarsus. (D) Left forewing. (E-J) Dorso-lateral appendages and medio-internal appendage of phallosome, not in situ (E same male as in A). (K-M) Spermapore sclerite and distal part of spermathecal duct (K and M ventral view; L optical longitudinal section, lateral view).

(reared from nymphs), 9 nymphs, leg. C. Lienhard, and 21 nymphs, leg. B. Hauser (MHNG, record published by Lienhard, 1996); Morocco, Middle Atlas, S of Taza, region of Daya Chiker, cave "gouffre du Friouato", 1450 m a.s.l., on rocky wall of cave covered by green algae, not far from cave entrance; 15.JUN.1990. – 1 nymph (MHNG) (mentioned as *Prionoglaris* spec. by Lienhard, 1988); same cave; 1.OCT.1979; leg. P. Strinati & V. Aellen.

Remark: An insect-pathogenic fungus was described from one nymph from the type locality in southern France by Keller (2011).

Prionoglaris* cf. *stygia

Previous records: Records of females or nymphs (and in one case a damaged male) as listed in detail by Lienhard (1988) from France, Germany (damaged male, phallosome lost), and nymphs from Portugal listed by Lienhard (1988) as *Prionoglaris* spec.

Additional records: 9 nymphs (MHNG, unpublished record); France, Savoie, St Christophe la Grotte, cave "Echelles Inférieure" (also called "Grands Goulets"), 570 m a.s.l.; 10.MAY.2018; leg. J. Lips. – 3 nymphs (MHNG, unpublished record); France, Savoie, St

Christophe la Grotte, cave "Perret" (also called "Fontaine Noire"), 470 m a.s.l.; 12.MAY.2018; leg. J. Lips. – 1 nymph (MHNG, unpublished record); France, Savoie, Vérel-de-Montbel, cave "Mandrin"; 26.MAY.2018; leg. J. Lips. – 2 nymphs (MHNG, unpublished record); France, Gard, Montclus, cave "Prével"; 6.MAY.2018; leg. J. Lips. – 4 nymphs (MHNG, unpublished record); France, Drôme, La Chapelle-en-Vercors, cave "Ferrières", 1020 m a.s.l.; 16.JUN.2017; leg. J. Lips. – 1 nymph (MHNG, unpublished record); France, Bouches-du-Rhône, Jouques, cave "Adaouste", 413 m a.s.l.; 02.FEB.2019; leg. J. Lips. – 1 nymph (MHNG, unpublished record); Switzerland, canton Schwyz, Muotathal, cave "Lauiloch", 460 m a.s.l.; 5.NOV.1996; leg. F. Auf der Maur. – Several nymphs (see Schneider *et al.*, 2012); Germany, Hessen and Rheinland-Pfalz, in nine caves. – 1 female and 90 nymphs (see Schneider & Weber, 2013); Luxembourg, near Mersch and near Muellerthal, in 11 caves. – Several nymphs; Luxembourg, collected by N. Schneider, considered as belonging to *Prionoglaris stygia*, used for molecular analysis by K. Yoshizawa (see Yoshizwa *et al.*, 2018, also Yoshizawa, *in litt.*). – 1 female (MHNG, unpublished record); Spain, Prov. Valencia, between Pego and Val de Ebo, 405 m a.s.l., macchia with few interspersed trees, under stones; 02.JUN.2010; leg. S. Huber & A. Schönhofer.

Prionoglaris dactyloides Lienhard, 1988

Previous records: Male records listed in detail by Lienhard (1988): Greece (Peloponnese and eastern Crete).

Prionoglaris cf. *dactyloides*

Previous records: Records of nymphs listed in detail by Lienhard (1988): Greece (Peloponnese).

Additional record: 10 nymphs (MHNG, unpublished record); Greece, eastern Crete, between Lassithiou and Tzermiado, near Ag. Timios, 1100-1200 m a.s.l., under stones; 10.APR.1998; leg. K. Thaler & B. Knoflach.

Prionoglaris lindbergi Badonnel, 1962

Previous records: 1 nymph holotype (see Badonnel, 1962) mounted on two slides (MHNG); Afghanistan, Karghaleh (above Kotouk, Ghourband valley), under stone, 3100 m a.s.l.; 06.AUG.1957; leg. Lindberg.

Prionoglaris kapralovi sp. nov.

Previous records: Armenia, see description above.

Prionoglaris spec.

Previous records: Records of females or nymphs listed in detail by Lienhard (1988): Former Yugoslavia (exact locality not known), Turkey.

Additional records: 2 nymphs (MHNG, unpublished record); Greece, western Crete, near Georgioupolis, between boulders, 100 m a.s.l.; 29.MAR.1999; leg. K. Thaler & B. Knoflach. – 1 nymph (MHNG, unpublished record); Greece, Island of Samos, road from Platanakia to Manolates, below Manolates, "valley of the nightingales", forest near river, 80 m a.s.l.; 26.NOV.1991; leg. B. Hauser. – 1 nymph (MHNG, unpublished record); Greece, Island of Rhodos, Petaloudes, Ag. Kalopetra, under stones in forest of pine trees and broad-leaved trees, 300 m a.s.l.; 09.APR.1996; leg. B. & K. Thaler. – 1 nymph (MHNG, unpublished record); Greece, Epirus, Timfi Mountains, above Mikro Papingo, under stones in rocky forest (limestone); 10.SEP.1996; leg. K. Thaler & B. Knoflach. – 3 nymphs (MHNG, unpublished record); Greece, Oros Iti, near Lamia, above Ipati, 1300 m a.s.l., limestone boulders; 18.SEP.1997; leg. K. Thaler & B. Knoflach. – 3 nymphs (see Georgiev & Ivanova, 2018a); Greece, Island of Corfu, in two caves. – Several nymphs; Greece, Island of Crete; leg. C. Lienhard; used for molecular analysis by K. Yoshizawa (see Yoshizwa *et al.*, 2018, also Yoshizawa, *in litt.*; identified as sp. 249). – Numerous nymphs (see Georgiev & Ivanova, 2018b; identified as *Prionoglaris* cf. *stygia*); Bulgaria, in several caves. – Several nymphs (see Georgiev, 2019); Bulgaria, in caves. – 1 nymph; Turkey, N of Adana, mountain E of Aksaray; leg. K. Yoshizawa; used for molecular analysis by K. Yoshizawa (see Yoshizwa *et al.*, 2018, also Yoshizawa, *in litt.*; identified as sp. 468).

Remark: Specimens of *Prionoglaris* spec. from Portugal listed by Lienhard (1988) are here considered as belonging to *Prionoglaris* cf. *stygia* (see above), and the single nymph recorded from the Moroccan cave "Gouffre du Friouato" belongs to *P. stygia* (see above).

DISCUSSION

Following the discovery of the new species *P. kapralovi*, the diagnosis not only of the genus *Prionoglaris* but also of the subfamily Prionoglaridinae has to be slightly modified, because the characteristic membranous vesicle on the inner side of the anterior pretarsal claw is absent in this species. The presence of a membranous extension on this claw in all other members of the subfamily Prionoglaridinae, and also in the fossil genus *Palaeosiamoglaris* from Cretaceous Burmese amber, was mentioned in the Remarks following the description of the new species. The sustained presence of this character since the mid-Cretaceous, i.e. during at least 100 million years, suggests that this structure has an important function in the life of these insects.

In other psocids possessing membranous extensions on pretarsal claws, as the pulvilli in the psocomorphan families Caeciliusidae and Ectopsocidae (symmetrically arranged on both claws of each pretarsus), these structures have an adhesive function enabling them to move on

smooth surfaces. In these families membranous pulvilli are also present in nymphs, and practically no variability concerning these adhesive organs has been observed among or within genera (Lienhard, 1998).

Our knowledge of the biology of Prionoglaridinae is very limited and the function of the membranous extension of the anterior pretarsal claw is unknown. In contrast to the above mentioned families, this membranous extension is absent in nymphs of the genus *Prionoglaris* (nymphs of the other genera of Prionoglaridinae are not known), as is the basal tooth of the posterior claw (Lienhard, 1988, 1998), which is usually present in adults of this genus (Fig. 3C), but absent in *P. kapralovi* sp. nov. (Fig. 2D). No difference in the biology of nymphs and adults in this genus is known that can explain this difference in claw morphology. However, important morphological differences in the mouthparts of nymphs and adults of *Prionoglaris* (see Lienhard, 1988, 1998) suggest that considerable differences in their mode of life exist.

The absence of a membranous vesicle and of a basal tooth in pretarsal claws of adults of *P. kapralovi* sp. nov. has to be considered as a neotenic character but its biological function remains enigmatic. Although the apomorphic neotenic absence of the membranous extension of the anterior claw and the basal tooth of the posterior claw in adults of this species is unique, it does not justify the formal establishment of a new supra-specific taxon.

The above remarks on the variability of some characters also show that a further splitting at species level, by recognizing a somewhat particular Moroccan cave population as a new species, would clearly be premature. However, the relative high variability of some morphological characters and the considerable molecular differences observed by Yoshizawa *et al.* (2018) between nymphs of three populations of *Prionoglaris* in Luxembourg (see Distribution, under *Prionoglaris* cf. *stygia*), Greece and Turkey (*Prionoglaris* spec.: sp. 249 and sp. 468 respectively) suggest the existence of some cryptic species in this genus (Lienhard, 2020: 7). Nonetheless, it cannot be ruled out that sp. 249 from Greece belongs to *P. dactyloides* and sp. 468 from Turkey to *P. kapralovi* sp. nov. It would therefore be very interesting to carry out a combined molecular and mophological study of *Prionoglaris* that also includes the Moroccan and Armenian populations.

The above overview on the known distribution of the genus, including records of nymphs, encourages to collect at these localities again and thereby obtain a more diverse material for molecular studies. In view of the scarcity of adults directly captured in nature, indispensable comparative morphological studies based on adults should be facilitated by rearing nymphs. A simple method for rearing nymphs has been described by Lienhard (1988).

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REFERENCES

Azar D., Huang Diying, El-Hajj L., Cai Chenyang, Nel A., Maksoud S. 2017. New Prionoglaridídae from Burmese amber (Psocodea: Trogiomorpha: Prionoglaridetae). *Cretaceous Research* 75: 146-156.

Badonnel A. 1962. Contribution à l'étude de la faune d'Afghanistan. 36. Psocoptères. *Kungliga fysiografiska Sällskapets i Lund Förhandlingar* 32: 1-6.

Badonnel A., Lienhard C. 1994. Psocoptera (pp. 301-305). *In*: Juberthie C., Decu V. (eds). Encyclopaedia Biospeologica, tome I. *Société de Biospéologie, Moulis,* XII + 834 pp.

Baz A. 2003. Catalogo provisional de los Psocopteros de Andalucia (Insecta, Psocoptera). *Boletin de la Asociacion Española de Entomologia* 27: 13-39.

De Moya R.S., Yoshizawa K., Walden K.K.O., Sweet A.D., Dietrich C.H., Johnson K.P. 2021. Phylogenomics of parasitic and non-parasitic lice (Insecta: Psocodea): combining sequence data and exploring compositional bias solutions in next generation datasets. *Systematic Biology*, 70: 719-738.

Enderlein G. 1909. Biospeologica. XI. Copeognathen (Erste Reihe). *Archives de Zoologie expérimentale et générale* (5)1: 533-539, pl. XVIII.

Georgiev D. 2019. A case study on the barkfly fauna of Vrachansky Balkan Nature Park (Insecta: Psocoptera) (pp. 35-38). *In*: Bechev D., Georgiev D. (eds). Faunistic diversity of Vrachansky Balkan Nature Park. Part 2. *ZooNotes* Supplement 7: 1-190.

Georgiev D., Ivanova V. 2018a. Study of the Psocoptera fauna of Corfu (Kerkyra) Island, Greece. *Parnassiana Archives* 6: 55-62.

Georgiev D.G., Ivanova V.I. 2018b. Psocoptera records from caves of Bulgaria. *Bulletin of the Natural History Museum Plovdiv* 3: 1-2.

Keller S. 2011. *Pandora psocopterae*, a new species of insect-pathogenic Entomophthoraceae (Fungi, Entomophthoromycetes) from France. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 84: 181-183.

Lienhard, C. 1988. Vorarbeiten zu einer Psocopteren–Fauna der Westpaläarktis. IV. Die Gattung *Prionoglaris* Enderlein (Psocoptera: Prionoglaridídae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 61: 89-108.

Lienhard C. 1996. Psocoptères nouveaux ou peu connus de quelques îles atlantiques (Canaries, Madère, Açores, Ascension) et de l'Afrique du Nord (Insecta: Psocoptera). *Boletim do Museu Municipal do Funchal (Historia Natural)* 48(267): 87-151.

Lienhard C. 1998. Psocoptères euro-méditerranéens. *Faune de France* 83: I-XX, 1-517.

Lienhard C. 2004. *Siamoglaris zebrina* gen. n., sp. n., the first representative of Prionoglarididae from the Oriental Region (Insecta: Psocoptera). *Revue suisse de Zoologie* 111(4): 865-875.

Lienhard C. 2011. A new species of *Siamoglaris* from Thailand with complementary description of the type species (Psocodea: 'Psocoptera': Prionoglarididae). *Revue suisse de Zoologie* 118(2): 293-306.

Lienhard C. 2020. Stories behind names – the insect family Prionoglarididae (Psocodea: 'Psocoptera'). *Psocid News* 22: 3-15.

Lienhard C., Smithers C.N. 2002. Psocoptera (Insecta): World Catalogue and Bibliography. *Instrumenta Biodiversitatis* 5: I-XLI, 1-745.

Lienhard C., Holusa O., Grafitti G. 2010a. Two new cave-dwelling Prionoglarididae from Venezuela and Namibia (Psocodea: 'Psocoptera': Trogiomorpha). *Revue suisse de Zoologie* 117(2): 185-197.

Lienhard C., Oliveira do Carmo T., Lopes Ferreira R. 2010b. A new genus of Sensitibillini from Brazilian caves (Psocodea: 'Psocoptera': Prionoglarididae). *Revue suisse de Zoologie* 117(4): 611-635.

Schneider N., Weber D. 2013. Staubläuse (Insecta, Psocodea, 'Psocoptera') aus Höhlen des Grossherzogtums Luxemburg. *Ferrantia* 69: 258-263.

Schneider N., Zaenker S., Dorow W.H.O. 2012. Staubläuse (Psocodea, ‚Psocoptera') aus zoologischen Untersuchungen in Hessen und den angrenzenden Gebieten. *Hessische Faunistische Briefe* 31(1-2): 1-30.

Yoshizawa K. 2005. Morphology of Psocomorpha (Psocodea: ‚Psocoptera'). *Insecta Matsumurana* (N. S.) 62: 1-44.

Yoshizawa K., Lienhard C. 2020. †Cormopsocidae: A new family of the suborder Trogiomorpha (Insecta: Psocodea) from Burmese amber. *Entomological Science* 23: 208-215.

Yoshizawa K., Lienhard C., Johnson K.P. 2006. Molecular systematics of the suborder Trogiomorpha (Insecta: Psocodea: 'Psocoptera'). *Zoological Journal of the Linnean Society* 146: 287-299.

Yoshizawa K., Ferreira R.L., Kamimura Y., Lienhard C. 2014. Female penis, male vagina, and their correlated evolution in a cave insect. *Current Biology* 24(9): 1006-1010.

Yoshizawa K., Johnson, K.P., Sweet A.D., Yao I., Ferreira R. L., Cameron S.L. 2017. Mitochondrial phylogenomics and genome rearrangements in the barklice (Insecta: Psocodea). *Molecular Phylogenetics and Evolution* 119: 118-127.

Yoshizawa K., Ferreira R.L., Yao I., Lienhard C., Kamimura Y. 2018. Independent origins of female penis and its coevolution with male vagina in cave insects (Psocodea: Prionoglarididae). *Biology Letters* 14: 20180533. DOI: 10.1098/rsbl.2018.0533

Yoshizawa K., Lienhard C., Yao I., Ferreira R.L. 2019. Cave insects with sex-reversed genitalia had their most recent common ancestor in West Gondwana (Psocodea: Prionoglarididae: Speleketorinae). *Entomological Science* 22: 334-338.

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Hydromedusae observed during night dives in the Gulf Stream

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Abstract: Hydromedusae were photographed and collected during 75 night-time dives in the Gulfstream off Florida. Most of the collected material was used to obtain DNA extracts and subsequently to determine part of the mitochondrial 16S rRNA gene, a barcode marker preferentially used for hydrozoans. The morphological data and the 16S barcodes permitted us to identify 46 species and 6 additional species nameable only to the genus level. Photos and descriptions are provided for all of them and the taxonomy and species status discussed. Six new species are described: *Pandeopsis prolifera* n. spec., *Zanclea mayeri* n. spec., *Corymorpha floridana* n. spec., *Staurodiscus luteus* n. spec., *Octophialucium irregularis* n. spec., *Solmaris flavofinis* n. spec. The new family Wuvulidae is proposed for the genus *Wuvula* Bouillon, Seghers & Boero, 1988. The new name *Aequorea neocyanea* is introduced for *Zygodactyla cyanea* L. Agassiz, 1862 to avoid a secondary homonymy with *Aequorea cyanea* de Blainville, 1834. *Zygodactyla cyanea* was considered to be a synonym of *Aequorea forskalea* Péron & Lesueur, 1810 for most of the 20th century, but we present arguments that it should be kept distinct from the latter and it must be transferred to the genus *Aequorea*. The genus *Otoporpa* Xu & Zhang, 1978 is regarded here as congeneric with *Pegantha* Haeckel, 1879 and its type species *Otoporpa polystriata* Xu & Zhang, 1978 is therefore changed to *Pegantha polystriata* (Xu & Zhang, 1978) new comb. *Dipleurosoma brooksii* Mayer, 1910 is recognized as a new synonym of *Staurodiscus kellneri* (Mayer, 1910); *Staurodiscus heterosceles* Haeckel, 1879 as a new synonym of *Staurodiscus tetrastaurus* Haeckel, 1879; *Orchistoma agariciforme* Keller, 1884 and *Tetracannota collapsum* Mayer, 1900 both as new synonyms of *Orchistoma pileus* (Lesson, 1843). The following Indo-Pacific species are newly recorded for the Atlantic Ocean: *Pandeopsis ikarii* (Uchida, 1927), *Aequorea taiwanensis* Zheng *et al.*, 2009; *Zygocanna apapillatus* Xu, Huang & Guo, 2014; *Gastroblasta timida* Keller, 1883; *Cunina becki* Bouillon, 1985; and *Pegantha polystriata* (Xu & Zhang, 1978). The 16S sequences also permitted us to discover several new links with polyp stages, this for *Cirrhitiara superba* (Mayer, 1900), *Euphysilla pyramidata* Kramp, 1955, *Zancleopsis dichotoma,* and *Melicertissa mayeri* Kramp, 1959. Detailed, high resolution photos of living medusae were found to be very useful for taxonomic purposes and are mostly preferable to preserved, damaged specimens obtained with plankton nets. Photos of living animals also permit us to better document material used to determine 16S barcodes and make the latter useable for taxonomic revisions.

Keywords: Cnidaria - Hydrozoa - Florida - blackwater diving - 16S DNA barcodes - taxonomy.

INTRODUCTION

Identifying hydromedusae can be a challenge, notably because the most important and still heavily used monographs of Kramp (1959a, 1968) have become somewhat dated. This not only because many new species have been discovered meanwhile, but also because the taxonomy has evolved and new diagnostic traits are being used. Whatsoever, there are no modern, comprehensive monographs with ocean-wide scopes like Kramp's and these remain an essential tool for taxonomists and plankton ecologists. Even the monograph of Mayer (1910) remains indispensable for systematists as it summarizes the entire older literature.

It is unlikely that in the near future comparable monographs will ever be published, above all because of copyright problems and because modern electronic databases offer more possibilities and flexibility, provided that they cover all species comprehensively. An outstanding example for such a taxonomic database is the AntWeb (AntWeb, 2021) and its taxonomic companion AntCat (Bolton, 2021). A comparable website for marine organisms is the "World Register of Marine Species"

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(WoRMS Editorial Board, 2021; Schuchert, 2020). However, there is still a long way to go until the WoRMS database can replace taxonomic monographs because it is still very incomplete. Although the currently accepted species names of Hydrozoa are nearly all entered in the WoRMS database, only a minority of species have suitable illustrations and/or links to recent publications with descriptions and figures. This absence cannot easily be overcome as for many hydrozoan species there exist simply no suitable illustrations. Above all, we generally lack good photos of living hydromedusae, photos showing sufficient details that can be used for taxonomic comparisons and that represent citable works that can be used as a permanent reference. More photos will allow for a better comparison of populations and assessment of geographic variation. There exist many good photos of hydromedusae in the internet, but they are too ephemeral for scientific purposes. A way to overcome this has been presented in Schuchert (2017a, b) who suggested creating archived electronic documents with a DOI number for specimens used to obtain DNA sequences published in GenBank. While this approach is useful especially for non-specialists, it is highly desirable to have many more published photos of living medusae identified by experts and accompanied by DNA barcodes (comp. e.g. Lindsay *et al*., 2017; Schuchert, 2017a, 2018). Unfortunately, many 16S barcodes deposited in GenBank lack information on how the animal was identified or no voucher specimen is available, too often not even the provenance is given (Marques *et al*., 2013). It is thus impossible to verify these identifications and the sequences get valueless if they are in conflict with more recent results.

Photos of living medusae – whole animals and details – present clear advantages over drawings and reconstructions made from preserved material collected with plankton nets (see e.g. Larson *et al.*, 1991; Mills *et al*., 1996; Wrobel & Mills, 1998; Raskoff *et al.,* 2003, 2005; Lindsay *et al.*, 2008, 2017; Schuchert, 2018). Net-collected samples are nearly always damaged or distorted, the subsequent preservation lets the specimens shrink, the colours fade, the statocysts regularly get dissolved, and the DNA is usually destroyed. This renders morphological comparisons often rather difficult.

The aim of the present work was therefore to document, identify, DNA barcode, and discuss the taxonomy of hydromedusae observed and photographed *in situ* off the coast of Florida.

As many medusae make diel vertical migrations (Mills, 1983; Buecher & Gibbons, 2003; Benovic *et al.*, 2005 and references therein), these species can only be seen by SCUBA divers during night-time (black water dives, comp. Hammer, 1975; Raskoff *et al*., 2003; Madin *et al*., 2013). This method is indeed very promising and several rarely reported medusae species were encountered [see *e.g.* also Nonaka *et al.* (2021) for a similar study on fish larvae].

MATERIAL AND METHODS

Sampling and photographing

All photography and sampling in Florida were done by RC during drift dives beginning at about sunset (civil twilight). The starting point was always approximately 5.5-12 km east of Palm Beach (USA, Florida) at approximately 26.7°N latitude. Starting bottom depths were between 150-200 m. Specimens were collected between the surface and 20 m depth with the great majority collected at 8-12 m. The divers drifted in a Northerly direction for 80 to 120 minutes, resulting in drifts of 2 to 17 km, depending on the drift time, strength of the current and relative location of the Gulf Stream. The average drift was about 8 km, diving depth 10-12 m. The approximate WGS84 coordinates are 26.70, -79.94 to 26.78, -79.94.

All specimens were photographed using a Nikon D800e with a Nikon AF Micro-NIKKOR 60 mm f/2.8D Lens. The camera housing was Nauticam D800, with 2 Ikelite DS161 strobes and two FixNeo 1500 lumen lights.

Specimens were collected in numbered (BFLA numbers), disposable, zip lock bags and preserved for DNA analysis in 95% ethanol or in 4% formaldehyde solution for voucher specimens (UF numbers). The material was then deposited in the Florida Museum of Natural History (USA, FL, Gainsville) and made available to PS.

For the medusae which were photographed but could not be collected, the size was estimated by RC. However, for most specimens photographed but not collected, especially prior to February 2019, estimates were not recorded and are thus not provided here.

Only a selection of the photos taken are shown here. The whole set has been deposited in both the Florida Museum of Natural History and the Muséum d'Histoire naturelle of Geneva (MHNG) where they will be entered in their collection management database.

The observed specimens are listed separately for each species in the section "Examined material". Each record starts with the field number (BFLA) if collected, or with the observation date if not collected. Sometimes a part of or the whole specimen was also preserved in formalin and deposited as voucher in the Florida Museum of Natural History. The catalogue numbers are given as UF-######. Because formalin-fixed voucher material is only available for a minority of the specimens, the field numbers (BFLA) in this work are used to refer to a particular sample. All specimens and observations for which no locality is specified came from the area given above. For some additional comparison material the provenance is given.

Species identifications

Published works used to identify the species are given in the synonymies. Only studied publications are given. In the paragraph entitled "Observations" the

actual observations and characteristics of the available specimens(s) are given, it is not a generalized description of the species. Not all observed species are reported here. Specimens that were not identifiable to species level and were also not collected for DNA barcoding have been omitted. In this study, only hydromedusae are presented. The Siphonophorae will be treated in a separate publication.

DNA barcoding

Methods for obtaining about 600 bp of the mitochondrial 16S gene as well maximum likelihood analyses are given in Schuchert (2014, 2018, 2019). The DNA extracts are kept by the Muséum d'Histoire naturelle of Geneva in their DNA collection (kept at -20°C, dissolved in TE buffer).

All new sequences have been deposited in the GenBank database with the accession numbers MW528627 to MW528734. The obtained 16S barcode sequence were compared to existing sequences in Genbank using the blastn search function (Johnson *et al*., 2008) as implemented in the website of GenBank (https://blast.ncbi.nlm.nih.gov). The resulting list was then sorted according to the percent identity of the sequences. For individual pairwise sequence comparisons, the two sequences were a ligned using Bioedit Sequence Alignment Editor (Hall, 1999) and the integrated ClustalW tool using default settings (Larkin *et al.*, 2007). After truncation to eliminate single stranded ends, the pairwise percent identities (p-values) were calculated using the corresponding function in BioEdit.

Additional examined comparison material

Aequorea forskalea Péron & Lesueur, 1810

Alcohol preserved sample MHNG-INVE-0055261; Mediterranean; collected before 1900; diameter ca. 10 cm, much fragmented, with gonads, about 100 radial canals. – Alcohol preserved sample MHNG-INVE-0055271; Mediterranean, Bay of Villefranche-sur-Mer; collected before 1895; det. C. Hartlaub; immature, 23 mm, ~48 radial canals.

Aequorea spec.

Pieces from two alcohol preserved medusae obtained from L. Leclère; Mediterranean, Bay of Villefranche-sur-Mer; collected 15-MAR-2017; 4-5 cm diameter, about half as many tentacle bulbs as radial canals; DOI of photos 10.5281/zenodo.4298436 and 10.5281/zenodo.4298454; used to obtain 16S sequence MW528733 and MW528734.

Aequorea macrodactyla (Brandt, 1834)

Alcohol preserved sample MHNG-INVE-55440; ca. 5 damaged specimens; Indonesia, Bay of Ambon; collected 1890; Material of Maas (1905).

Aequorea vitrina Gosse, 1853

One living, much damaged medusa obtained from J. J. Soto Angel and L. Martell; collected 27-MAR-2019; Norway, Hordaland, near Bergen, WGS84: 60.4567, 4.9339; ca. 10 cm diameter, >100 radial canals, about 5 times as many tentacles as radial canals; used to obtain 16S sequence MW528629.

GENERAL RESULTS AND DISCUSSION

Using close-up photos taken during 75 dives in the time period from 19 September 2018 to 18 June 2020 (123.5 hours total diving time) combined with the 16S RNA gene sequences it was possible to distinguish at least 56 species of hydromedusae. Of these 56 species, 52 are treated in the following taxonomic part, but 6 of them could only be identified to genus level (Appendix 1). Six new species are described. Four morphotypes are not treated here as either not enough data and/or material was available to identify them.

The approach to take several photos *in situ* and then use a tissue sample for DNA barcoding proved to be very satisfactory. Good photos taken at several angles and distances mostly permited us to see all relavant taxonomic traits of these transparent animals. As in preserved samples, it is of course important that the animals are sufficiently mature, *viz*. gonads are present. Such photos were actually often more useful than preserved specimens. Preserved medusae, notably those obtained with plankton nets, are regularly distorted and damaged and often only suitable for schematic drawings that need to be based on several specimens. Photos of living specimens are always preferable as they can provide taxonomically important information which is not well conveyed in drawings, e.g. colours and tissue opaqueness. Also the bell shape, mesoglea thickness, and the proportions are better examined in living material as they aremostly not well preserved. A disadvantage of the photographic/*in situ* approach is that microscopic details – like statocysts, nematocyst groups, and cirri – are less well visible and examinable. Sometimes these details could be examined in the alcohol preserved sample before DNA extraction. Another drawback, but which is also a problem in net-material, is the low number of specimens and the absence of fully mature animals making it regularly impossible to obtain a complete idea of the morphological variability of a species (comp. *Aequorea* species).

Recent molecular analyses showed that many hydroids have a very high genetic diversity and are likely species complexes (Moura *et al*., 2008; Schuchert, 2014; Montano *et al*., 2017; Maggioni *et al*., 2018, 2020; Postaire *et al*., 2017; Miglietta *et al*., 2018a; Boissin *et al*., 2018). Our medusa samples were all collected in a quite narrow region, but several morphospecies proved to be composed of two or more deeply separated molecular clades (*Zancleopsis dichotoma*, *Laodicea undulata, Orchistoma*

pileus, *Pseudaegina rhodina*) or they were split here into sister species if the clades correlated with morphological differences (*Pandeopsis ikarii* and *P. prolifera* n. spec., *Proboscidactyla ornata* and *P. gemmifera*). An explanation for high intraspecific variation could be that the animals brought to the collecting site by the Gulf Stream originated from far apart sites and populations (see discussion under *Zancleopsis dichotoma*).

Our observations also revealed the presence of several Indo-Pacific species which have so far not been seen in the Atlantic Ocean: *Pandeopsis ikarii*, *Aequorea taiwanensis*, *Zygocanna* cf. *apapillatus*, *Gastroblasta timida*, *Cunina becki*, and *Pegantha polystriata*. *Thecocodium quadratum* was also found, but this surprising occurrence has already been reported by others (Kubota & Meldonian, 2016).

The new barcodes also permitted us to find similar sequences in GenBank obtained from hydroids and which are potentially the polyp stage of these medusae, or at least they will resemble them strongly (comp. Schuchert, 2016, 2018; Schuchert *et al.*, 2017). The 16S sequence of *Cirrhitiara superba* (Mayer, 1900) matched very closely the one obtained of a hydroid from Panama identified as *Thecocodium* spec. The 16S of *Euphysilla pyramidata* Kramp, 1955 matched closely a published sequence of a *Sphaerocoryne* polyp collected in the Maldives archipelago. The 16S barcodes of *Zancleopsis dichotoma* (Mayer, 1900) were related to ones of *Astrocoryne*

Table 1. 16S haplotype p-distances (% base pair differences in aligned sequence pairs) and number of haplotypes observed in the examined material. Only the species for which such a comparison was possible are listed.

species	p-distance within examined population	number of haplo-types	p-distances compared to haplotypes of the same species available in GenBank [GB number, locality]
Cytaeis tetrastyla	1.0-2.2	3	-
Pandeopsis ikarii	-	1	3.5 [MG136757, Japan]
Pandeopsis prolifera n. spec	2.3	2	-
Turritopsis nutricula	0.5	2	1.4-1.9 [EU624348, New England; MH029857 Panama]
Thecocodium quadratum	0.5	2	4.3-4.5 [FN422379, W Indian Ocean]
Proboscidactyla ornata	0.4-1.0	4	6.7-7.5 [EU305481, Caribbean; JQ715911, China]
Euphysilla pyramidata	0.2	2	-
Zanclea mayeri n. spec.	0.8-1.2	4	-
Zancleopsis dichotoma	0.5-6.2	5	-
Laodicea undulata	0.2-10.6	4	5.5-8.1[FJ55047, KY36396, KY36396; European coasts]
Staurodiscus kellneri	0.2-0.5	3	-
Staurodiscus tetrastaurus	0.2	2	-
Orchistoma pileus	0.5-8.1	7	-
Wuvula ochracea	0.2	2	-
Aequorea neocyanea	0.3-2.1	8	3.7-5.2 [MW528733, MW528734, Mediterranean]
Aequorea spec. 1	0.2-1.0	5	-
Aequorea taiwanensis	0.2-0.5	3	0.2-0.64 [JQ716019, JQ716019, Taiwan Strait]
Octophialucium aphrodite	0.8	2	-
Pseudaegina rhodina	0.2-7.8	4	-
Pegantha martagon	0.2-1.4	3	25 [MG979374, California]
Solmaris corona	1.7-3.2	3	-
Solmaris flavofinis	0.2	2	-
Solmundella bitentaculata	-	1	8.6-10.5 -14 [KX355407, Mediterranean; KF97740, China Sea; EU293998, Antarctica]
Aglaura hemistoma	0.9	2	2.0-5.0 [KP776748, Mediterranean; EU293984, Japan]
Rhopalonema velatum	0.2	2	0.2-4.3 (EU29399, Mediterranean; EU293993, Tierra del Fuego)
Geryonia proboscidalis	-	1	0.17-1.2 [KX355451, Mediterranean; EU293979, Japan; KT809331, Sea of Cortez]
Olindias tenuis	-	1	0.5 [MG979369, U.S. Virgin Islands]

cabela Maggioni *et al*., 2017, a hydroid found in the Red Sea and the Maldivian Archipelago. *Hebella venusta* (Allman, 1877) is likely the hydroid of *Melicertissa mayeri* Kramp, 1959 as their 16S are sufficiently similar. These results demonstrate again the value of 16S barcodes and well documented entries in GenBank for hydrozoan systematics. A taxonomically sound reference sequence database is also a prerequisite for new approaches using next generation sequencing of environmental DNA to monitor the biodiversity of a habitat [see e.g. Ames *et al.* (2021) for an eDNA study on jellyfish].

TAXONOMIC PART

Order Anthoathecata
Suborder Filifera
Family Bougainvilliidae Lütken, 1850
Genus *Bougainvillia* Lesson, 1830

Synonymy: See Schuchert (2007).

Diagnosis: Medusa with four perradial marginal bulbs bearing two or more identical tentacles, bulbs with or without ocelli; four perradial oral tentacles, usually branched and ending in nematocyst clusters; gonads interradial or adradial on manubrium, sometimes also along basal perradial extensions of the manubrium.
Hydroid colony stolonal or branched, more rarely hydranths sessile; perisarc terminating at base of hydranth or extending onto hydranth as pseudohydrotheca; hydranth cylindrical to spindle-shaped, tentacles in one or two closely approximated whorls, tentacle-bases never enveloped by pseudohydrotheca, tentacles alternately inclined up- and downward (amphicoronate). Gonophores develop into free medusae, arising singly or in clusters from stem, branches or stolons.

***Bougainvillia* spec.**
Fig. 1A-B

Examined material: BFLA3826; 1 specimen, 14-NOV-2018; bell height 5 mm; photographed and then preserved in alcohol for DNA extraction; 16S sequence MW528641.

Observations: Bell 5 mm high, higher than wide, mesoglea thick, apical mesoglea 1/4 of bell height, apex rather flat. Manubrium with cruciform base, oral region tubular, widest at base and thus like an inverted cone; four perradial oral tentacles arise well above mouth rim, trunk long, branched about 3 to 4 times, ending in spherical nematocyst knobs. Four gonads, male, interradial, encircling stomach entirely. Four radial canals and marginal bulbs, bulbs D-shaped (Fig. 1B), each with about eight filiform tentacles; dark, round ocelli on adaxial side of tentacle base.

16S Data: A blastn search with the partial 16S gene sequence (MW528641) did not give a close match, but the best five matches were *Bougainvillia* species. The sequence with the highest similarity (94% identity) was EU305470, obtained from a *B. fulva* collected in Japan (Kirsten Jensen, Kansas University, pers. com.). Others were *B. triestina* and *B. carolinensis* with about 92% identity. *Bougainvillia muscus* sequences differed even more, reaching only 87% identity.

Remarks: This *Bougainvillia* medusa could not be identified reliably. Morphologically, it resembles *B. carolinensis* (McCrady, 1859) and *B. muscus*

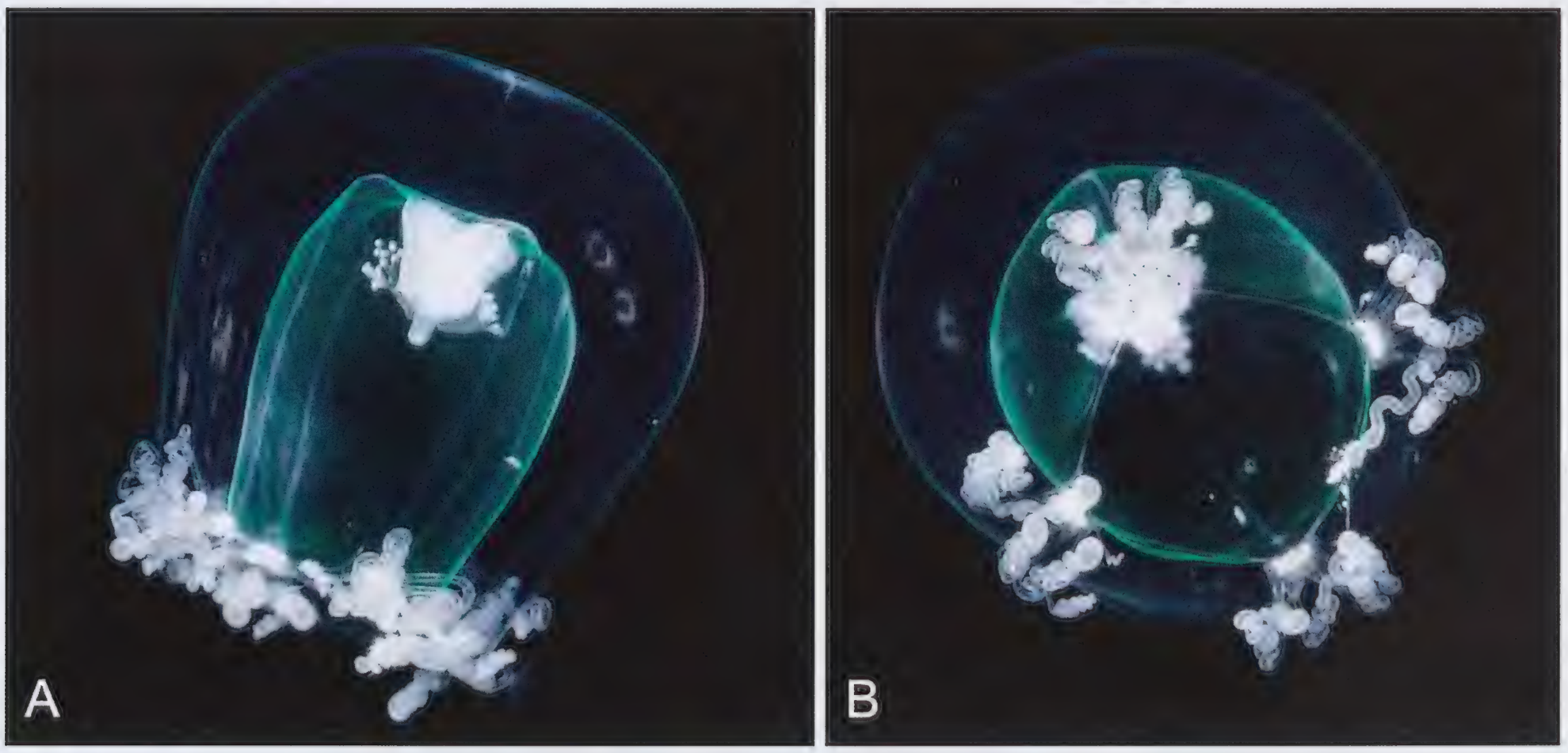


Fig. 1. *Bougainvillia* spec. of 14-NOV-2018, bell height 5 mm (A) Lateral view of whole animal. (B) Oral view.

(Allman, 1863). It differs from *B. carolinensis* (see descriptions in Mayer, 1910; Kramp, 1959a; Calder, 1971) in lacking the characteristic shape of the manubrium, which is widening from the aboral end towards the mouth. The manubrium of the present medusa is widest at the aboral end (Fig. 1A). *Bougainvillia muscus* medusae (for a description see Schuchert, 2007) differ in being smaller (1-4 mm), they have less tentacles per bulb (2-6), and the oral tentacles branch less (0-2).

Also, the 16S data argue against *B. carolinensis* and *B. muscus*. There are several 16S sequences of *B. muscus* available in GenBank (e.g. AM183126, AM411411), covering populations from Europe to New Zealand and with an intraspecific divergence of up to 1.5% base pair differences. The *Bougainvillia* medusa from Florida differed from *B. muscus* in 13% of the base pairs, and was thus far beyond the intraspecific divergence. The single available sequence from a *B. carolinensis* from Brazil (MG791827) did also not match (90% identity only). No morphological data are available for this sample and its identification cannot be verified.

Other *Bougainvillia* medusae known from the region can also be excluded based on their morphology. *Bougainvillia niobe* Mayer, 1894 buds medusae from the manubrium. These might not always be present, especially in mature animals (compare fig. 90 in Mayer, 1910), but the gonads are reportedly adradial and not interradial (Kramp, 1959a: 12). *Bougainvillia rugosa* Clarke, 1882 has medusae with unbranched oral tentacles and only 3 tentacles per bulb (Migotto, 1996).

The observed medusa thus likely belongs to an unnamed species, or a hydroid-based nominal species for which the adult medusa is not known yet. Using the 16S sequence will certainly in the future permit the identification of the hydroid (comp. Schuchert *et al.*, 2017; Schuchert, 2019), as well as additional growth stages and the females of the medusa, and thus give a more solid base for the description as a new species.

Family Cytaeididae L. Agassiz, 1862
Genus *Cytaeis* Eschscholtz, 1829

Synonymy: See Schuchert (2007).

Diagnosis: Medusa with spherical to oblong bell, four or more capitate oral tentacles arising well above mouth margin, medusa budding from manubrium. With four marginal tentacles, solid, tapering, in adults with broad, enlarged base adhering to exumbrella just above bell margin, no ocelli.

Hydroids monomorphic, arising from reticulate stolons covered by perisarc. Hydranths sessile, with one whorl of filiform tentacles below conical hypostome; base of hydranths often with a perisarc collar. Gonophores develop from stolons, liberated as medusa with four tentacles.

Cytaeis tetrastyla Eschscholtz, 1829
Fig. 2A-C

Cytaeis tetrastyla Eschscholtz, 1829: 104, pl. 8 fig. 2. – Schuchert, 2007: 275, fig. 32, synonymy, references, taxonomic details.

Examined material: BFLA4066; 1 specimen; 10-APR-2019; size 2 mm; preserved in ethanol for DNA extraction; 16S sequence MW528664. – BFLA4069; 1 specimen; 11-APR-2019; size 1.5 mm; photographed and preserved in formalin and deposited as UF-013780. – BFLA4073; 1 specimen; 11-APR-2019; 2 mm; preserved in ethanol for DNA extraction; 16S sequence MW528667. – BFLA4418; 1 specimen; 28-MAY-2020; size 4 mm; preserved in ethanol for DNA extraction; 16S sequence MW528725. – 16-NOV-2017; 1 specimen photographed, not collected.

Observations: *Cytaeis* medusa with bell height 1.5-2 mm, apical jelly not much thickened and without apical process, but often with apical funnel-like depression; subumbrella with shallow gastric peduncle. Manubrium spindle-shaped, reaching to velum level, with more than 10 capitate tentacles originating distinctly above mouth margin; in upper third of manubrium several medusa buds, in lower two thirds apparently with developing gonad. Four perradial tentacles, fully contracted about as long as bell height, solid, bases widened to ovoid bulbs which adhere just above bell margin, giving the impression of the tentacles being connected by a flared end (Fig. 2B); the tentacle arises at an acute angle to the bulb and curve towards aboral.

Distribution: Circumglobally in tropical to subtropical seas, partly oceanic (Schuchert, 2007). Type locality: Atlantic Ocean, south of Equator.

16S Data: The three obtained 16S haplotypes have a maximal divergence of 2.2% and are thought to represent intraspecific variation (Table 1). Blastn searches in GenBank did not yield matches at species-level identities. The closest matches were with several samples of *Cytaeis uchidae* Rees, 1962 from Japan (about 95% identity), followed by other *Cytaeis* species, though with lower identity values.

Remarks: The taxonomic situation and identification of *Cytaeis* medusae is currently not resolved (see discussion in Schuchert, 2007). The opinion of Bouillon *et al.* (2004) that the "*Cytaeis tetrastyla*-like"medusae should not be given a specific name until the taxonomy has been sorted out properly is still valid, in particular if they do not come from the tropical Atlantic Ocean. However, the current material does come from the same tropical waters of the Atlantic Ocean as the type material and no named or distinct *Cytaeis* polyps are known from this region. We can thus be reasonably sure that *Cytaeis tetrastyla* is most likely the correct name.

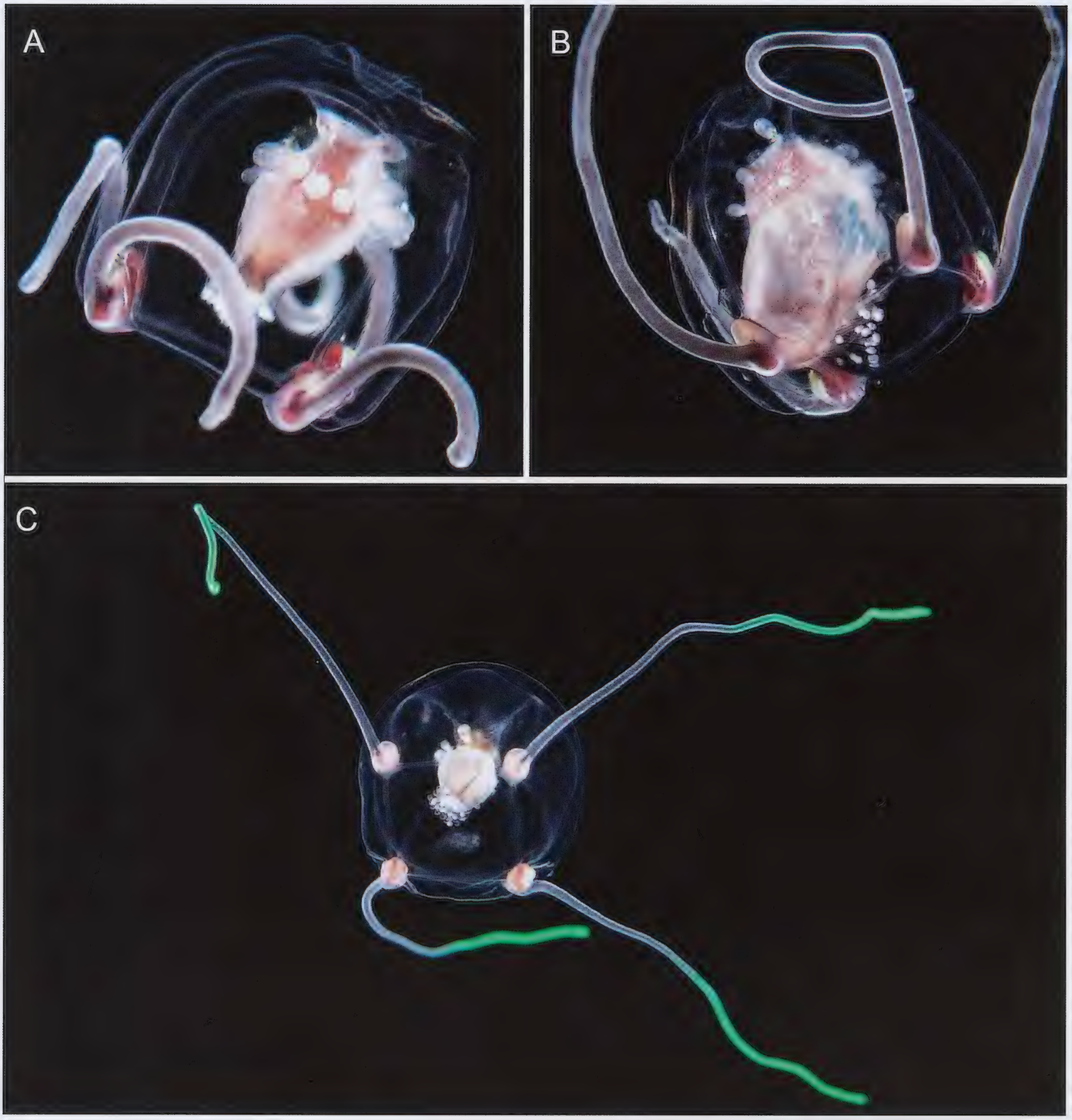


Fig. 2. *Cytaeis tetrastyla*, bell height 2 mm. (A) Lateral view, note medusa buds on upper part of manubrium, BFLA4066. (B) Lateral view with focus on the frontal exumbrella showing the typical flared tentacle bases of *Cytaeis* medusae, BFLA4073. (C) BFLA4069, note green tentacle tips, a colour likely due to interference effects and not pigments.

The taxonomic ambiguity relating to *C. tetrastyla* needs to be resolved using DNA sequence data of several populations and the present samples will hopefully contribute to this end.

Many cytaeidid medusae have a quite characteristic connection of the tentacles to the bell margin. The proximal ends of the tentacles are widened to an ovoid bulb which adheres along its long axis to the exumbrella just above bell margin, giving the impression of the tentacle being connected to the exumbrella by a flattened end (Fig. 2B).

The hydroid stage of this species is not known. A potential candidate is the *Cytaeis* hydroid from Bermuda Island described by Calder (1988).

Family Pandeidae Haeckel, 1879
Genus *Amphinema* Haeckel, 1879

Synonymy: See Schuchert (2007).

Diagnosis: Medusa with two long opposite tentacles; with or without ocelli; gastric peduncle absent; mostly with a considerable apical projection; with or without additional marginal small cirri or marginal rudimentary bulbs; with or without mesenteries; four simple oral lips, not or not much crenulated. Gonads on manubrium in adradial or interradial position, occasionally extending to the radial canals.
Hydroid colonies usually stolonal [except for one species of uncertain affinity, *Amphinema biscayana* (Browne, 1907)], hydranths with a well developed caulus, caulus longer than hydranth, covered by perisarc; hydranths without pseudohydrotheca, spindle-shaped, conical hypostome, one whorl of filiform, amphicoronate tentacles. Polyps bend over when disturbed. Gonophores arise either from cauli, stolons or both, released as free medusae.

Amphinema turrida (Mayer, 1900)
Figs 3A-D

Dissonema turrida Mayer, 1900: 44, pl. 2 figs 3-4. – Mayer, 1910: 116, pl. 10 fig. 1, pl. 22 fig. 1.
Stomotoca turrida. – Mayer, 1915: 199, pl. 1 fig. 1.
Amphinema turrida. – Schuchert, 2007: 312, fig. 48.

Examined material: 02-JUL-2018; 1 specimen photographed; approximately 6 mm; not collected.

Observations: *Amphinema* medusa, approximately 6 mm high, with elongated, folded gonads that extend along 5/6 of radial canals (Fig. 3A-B); manubrium about half the height of the subumbrella, simple cruciform mouth with a few folds; two opposite tentacles, long, hollow, base laterally compressed and clasping bell margin, no abaxial spur, large red abaxial ocellus; about 12 rudimentary bulbs on bell margin, each with a large, red ocellus (Fig. 3B). Adradial and interradial rudimentary bulbs bearing a thin cirrus originating in the middle of the bulb (Fig. 3C).

Distribution: Florida and Bahamas; Mediterranean; Torres Strait; Papua New Guinea; Japan; Pacific Side of Mexico; Chile (Schuchert, 2007). Type locality: USA, Florida, Dry Tortugas archipelago.

Remarks: *Amphinema turrida* has recently been redescribed and discussed by Schuchert (2007). Most Pacific populations lack the cirri and their status needs to be re-evaluated using genetic data.

Genus *Cirrhitiara* Hartlaub, 1914

Cirrhitiara Hartlaub, 1914: 284; type species *Tiara superba* Mayer, 1900, by monotypy.

Diagnosis: Pandeid medusa with solid apical projection; 4 or 8 large hollow marginal tentacles alternating with rudimentary marginal bulbs, each carrying a single lateral cirrus; all marginal bulbs with ocelli; gonads adradial, with diverging folds directed perradially, with interradial transverse fold connecting the adradial groups of gonads; with long mesenteries. Hydroid unknown.

Cirrhitiara superba (Mayer, 1900)
Figs 4A-D, 5

Tiara superba Mayer, 1900: 34, pl. 16 fig. 39.
Tiara pileata var. *superba.* – Mayer, 1910: 126, pl. 27 fig. 8, pl. 28 figs 3-4.
Tiara pileata f. *superba.* – Vanhöffen, 1913a: 416.
Cirrhitiara superba. – Hartlaub, 1914: 284, fig. 237. – Kramp, 1959a: 121, fig. 122. – Kramp, 1961: 97. – Kramp, 1968: 39, fig. 101.
not *Cirrhitiara superba.* – Thiel, 1938: 296, fig. 2. – Kramp, 1953: 267. – Van der Spoel & Bleeker, 1988: 167, fig. 8.

Examined material: BFLA4087; 1 specimen; 07-MAY-2019; preserved in ethanol for DNA extraction; 16S sequence MW528672. – 30-JUL-2018; 1 specimen photographed; not collected.

Observations: Pandeid medusa 7 mm high and 5 mm wide, bright pink manubrium and tentacle bulbs, apical process of variable size present, apical exumbrella with perradial furrows. Manubrium filling more than half of the volume of the subumbrella, mouth rim complexly folded. Gonads on stomach forming folds diverging from interradial, in each quadrant two adradial series of folds that are connected interradially by a transverse fold. Four broad radial canals, connected to stomach via funnel-like widenings. Four long, tapering, perradial tentacles, base laterally compressed and clasping bell margin, no abaxial spur, large red abaxial ocellus near abaxial end. Alternating with the tentacles three small bulbs, each with an abaxial ocellus and a thin cirrus usually originating laterally from bulb. All small bulbs of equal size.

16S Data: The partial 16S gene sequence (MW528672) obtained was used to search for similar sequences in GenBank using the blastn function. Similar sequences found were mostly from *Leuckartiara* species and other Pandeidae, giving sequence identities in the 90% range. However, there was also one sequence (MH361354) which had only a single mismatch in 599 aligned bases (99.8% identity, = 0.2 % divergence), a value which certainly represents intraspecific variation (reference values for Pandeidae acc. Schuchert, 2018, table 2). The matching sequence was obtained from a hydroid originating from Caribbean Sea close to Panama and identified as *Thecocodium* spec. (Miglietta *et al*., 2018b). The hydroid is described and depicted in the supplementary material of Miglietta *et al*. (2018b).

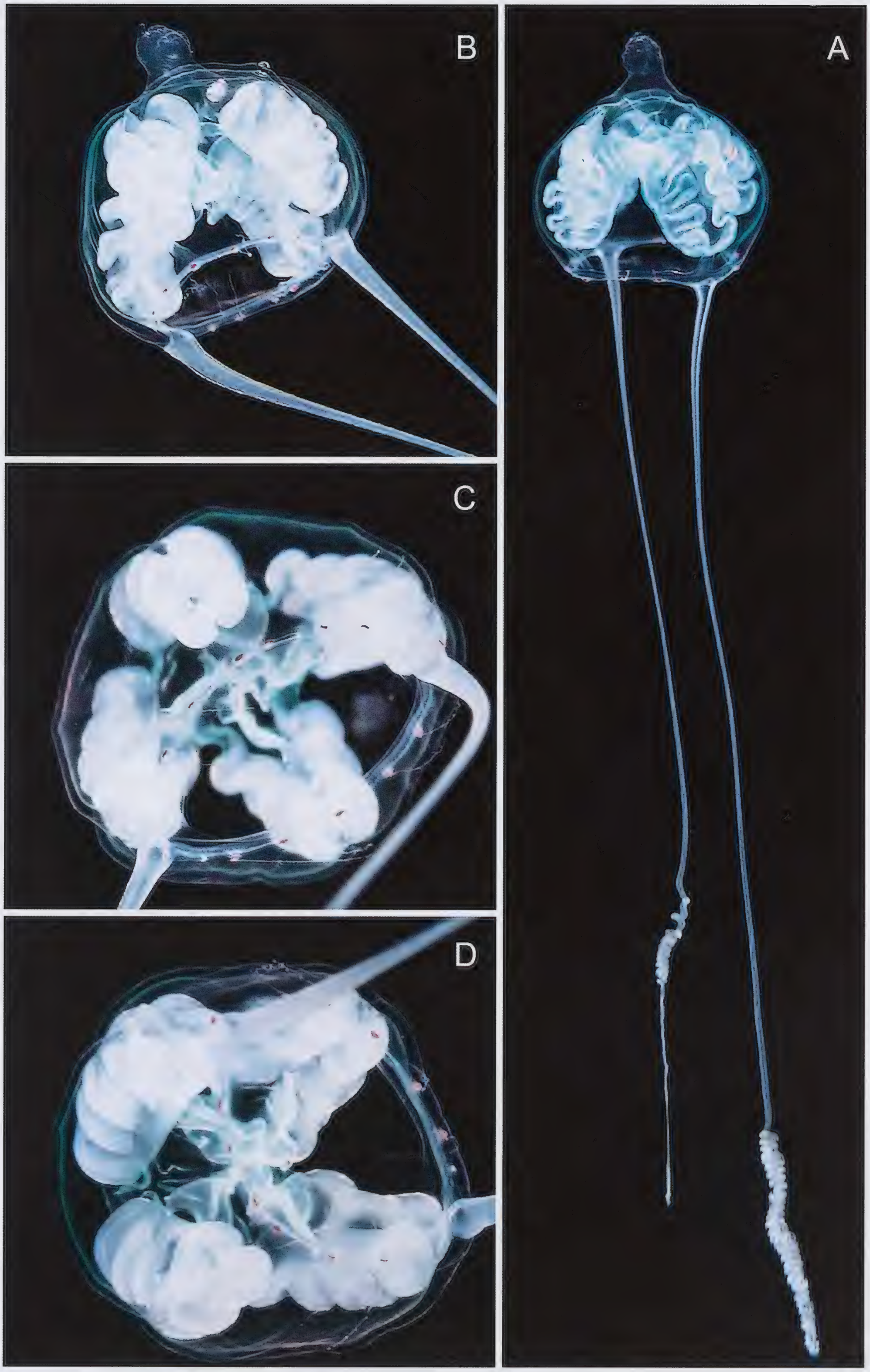


Fig. 3. *Amphinema turrida*, bell height approximately 6 mm. (A) Lateral view. (B-D) Oblique views from oral side, note the presence of thin cirri.

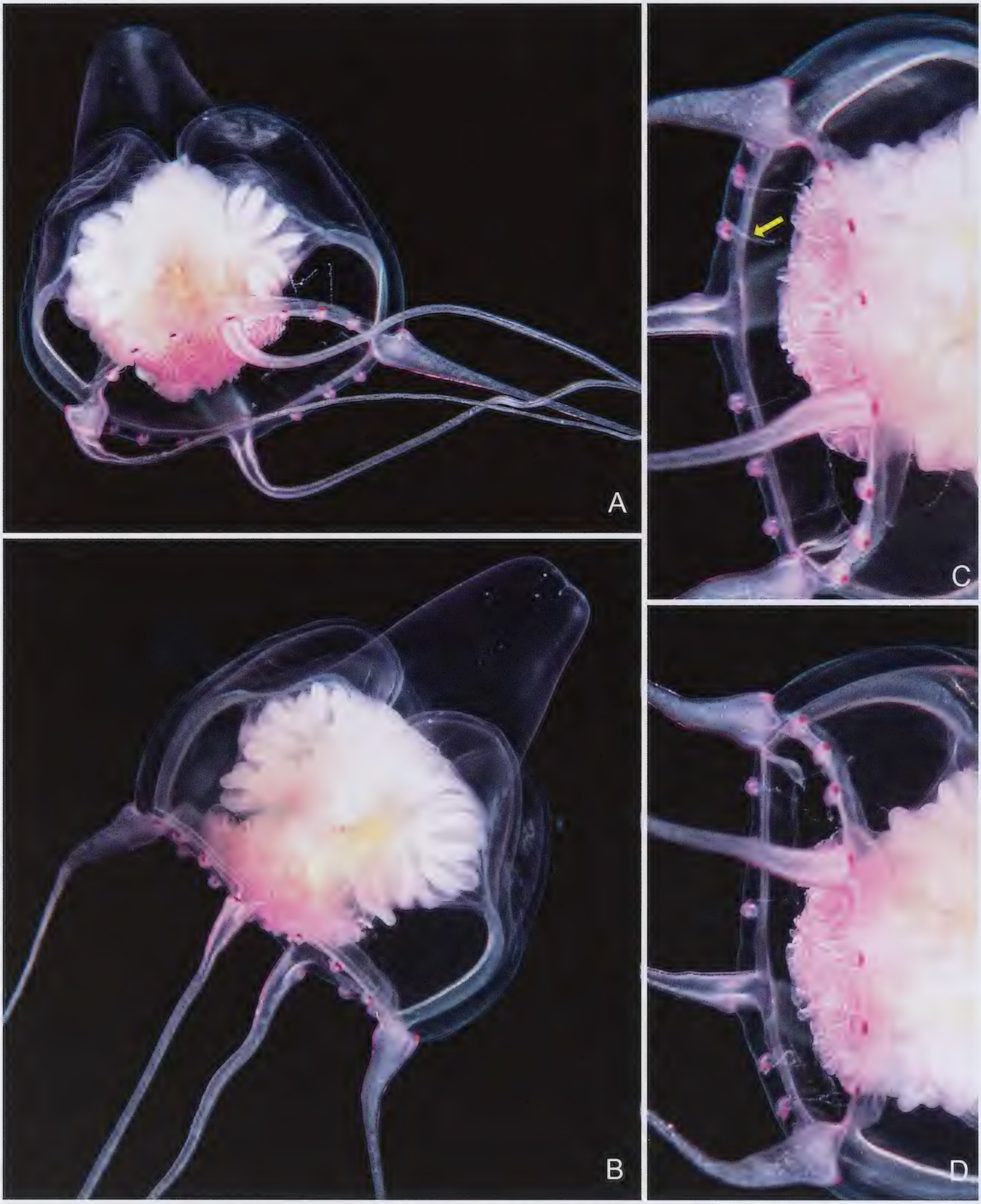


Fig. 4. *Cirrhitiara superba*, specimen BFLA4087, bell height 7 mm. (A-B) Lateral view. (C-D) Close up of bell margin, note cirri (arrow in C).

Fig. 5. *Cirrhitiara superba*, specimen observed in 2018 but not collected. The cirri are barely visible.

It is a polyp lacking tentacles. The typical capitate dactylozooids of the genus *Thecocodium* were not observed, which means that it could also belong to other genera with hydroids lacking tentacles, e.g. *Hydrichthys* (Pandeidae, see Schuchert, 2007).
The obtained 16S sequence did not cluster with any other genus of Pandeidae for which there were sequences available (Fig. 8), but this is due to the poor resolving power of the 16S marker above the genus level.

Remarks: *Cirrhitiara superba* has only rarely been reported. The identity of the present material is beyond doubt as it matches very well the descriptions in Mayer (1900, 1910). Moreover, it comes from the same region and the same continental shelf region as the type material.
Thiel (1938) identified a small (1 mm) juvenile medusa from Brazil as *C. superba*. His specimen had eight tentacles, the interradial ones being less developed. There were also 8 to (?) 16 rudimentary bulbs, each with a lateral cirrus. The presence of interradial tentacles – even less developed – argues against this being *C. superba.* Neither Mayer (1900, 1910) nor we observed interradial tentacles in *C. superba.* Vanhöffen (1913a), who had mostly young medusae obtained from Mayer, speaks of 8 tentacles in his largest medusae, but he was likely referring to both types of tentacles, *viz.* four large ones and four cirri.
Kramp (1953) thought that two medusae collected near the eastern coast of Australia belonged to *C. superba* despite they lacked cirri. Additionally, the interradial bulbs were larger than the adradial ones and no ocelli were observed. This makes the identification rather doubtful. The medusae are perhaps referable to *Leuckartiara fujianensis* Huang, Xu, Lin & Qiu, 2008 or *Leuckartiara neustona* Xu & Huang, 2004.
The medusa shown in Van der Spoel & Bleeker (1988: fig. 8) originating from Indonesia had thick cirri and 8 long tentacles and thus unlikely belong to the present species.

Distribution: Florida, Bahamas (Mayer, 1910). Records from Brazil (Thiel, 1938), north-eastern Australia (Kramp, 1953), and Indonesia (Van der Spoel & Bleeker, 1988) are likely misidentifications (see above). Type locality: USA, Florida, Dry Tortugas archipelago.

Genus *Merga* Hartlaub, 1914

Merga Hartlaub, 1914: 249; type species *Pandea violacea* Agassiz & Mayer, 1899 by original designation.
Tiarula Hartlaub, 1914: 253; type species *Tiara tergestina* Neppi & Stiasny, 1912 by original designation.
Mergintha Hartlaub, 1914: 250; type species *Mergintha lobianci* Hartlaub, 1914 by monotypy.
Janiopsis Bouillon, 1980: 328; type species *Janiopsis costata* Bouillon, 1980 by monotypy; invalid junior homonym of *Janiopsis* Rovereto, 1899 [Gastropoda, Buccinidae].

Diagnosis: Pandeid medusae with smooth or granulate adradial or interradial gonads, with mesenteries, stomach with cross-shaped base, manubrium not twisted, with simple or faintly crenulated oral lips; four, eight, or more tentacles, with or without rudimentary bulbs or tentacle-stumps, with or without ocelli.
Hydroids, where known, colonial, arising from tubular, ramified hydrorhiza, cauli slightly branched or not, with or without pseudohydrotheca, when present not enveloping tentacles, one whorl of filiform tentacles. Medusa buds arise from stems or stolons.

Merga violacea (Agassiz & Mayer, 1899)

Fig. 6A-E

Pandea violacea Agassiz & Mayer, 1899: 160. – Mayer, 1900: 34, pl. 1 fig. 1. – Bigelow, 1909: 205, pl. 41, figs 10-11. – Mayer, 1910: 119, text fig. 64, pl. 11 fig. 7, pl. 12 fig. 1.
Mergintha lobiancoi Hartlaub, 1914: 250, fig. 205. – Kramp, 1953: 265, synonym.
Merga violacea. – Hartlaub, 1914: 249, fig. 204, new combination. – Kramp, 1953: 265. – Kramp, 1959a: 116, fig. 106. – Kramp, 1961: 107. – Kramp, 1968: 41, fig. 104. – Schuchert, 2007: 355, fig. 69.
? not *Merga violacea.* – Menon, 1932: 7, pl. 1 fig. 10. [? = *Pandeopsis ikarii*]

Examined material: BFLA4006; 1 specimen; 26-NOV-2018; size 12 mm high, 10 mm wide, pink colour; photographed and preserved in ethanol for DNA

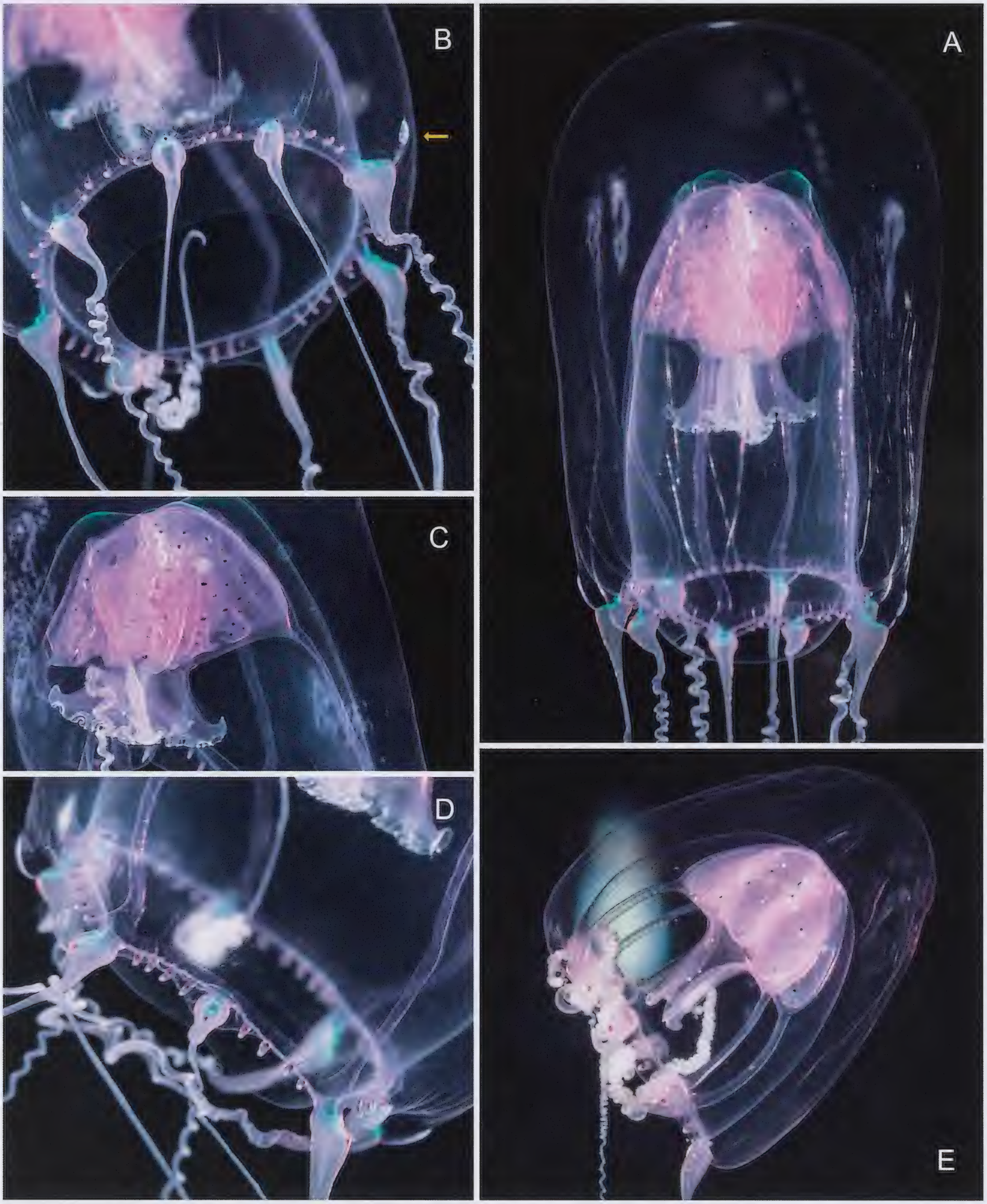


Fig. 6. *Merga violacea*. (A-D) Specimen BFLA4006, bell height 12 mm. (A) Lateral view of whole animal, note that the bell is somewhat contracted and more elongate than normal. (B) Bell margin seen from oral, note the flat abaxial spurs above some of the tentacle bulbs (arrow). (C) Lateral view of stomach. (D) Bell margin, note rudimentary bulbs with short tentacle stumps. (E) Lateral view of younger animal observed 30-Jun-2018, size approximately 7 mm.

extraction; 16S sequence MW528650. – 30-JUN-2018; 1 specimen photographed; size approximately 7 mm, pink, only 2 rudimentary bulbs between tentacle pairs; not collected. – 09-AUG-2018; 1 specimen photographed; size approximately 10 mm, pink; not collected.

Observations: Typical medusa of the genus *Merga*, up to 12 mm high, characteristic light pink-purple colour of manubrium and tentacles (Fig. 6A-E), without apical process but when fully grown with a thick apical jelly, shallow subumbrellar pockets present. Manubrium about half the height of subumbrella, very wide, connected for about half its length along the radial canals; stomach base and mouth cruciform, mouth rim slightly folded. Gonads on interradial surfaces of stomach, thin, smooth and not folded. Four radial canals broad, connected to stomach in its upper parts as mesenteries. Eight long, tapering tentacles, base laterally compressed and clasping bell margin, may be continued on exumbrella as an atypical, flat, abaxial spur (Fig. 6B); large red abaxial ocellus near abaxial end of bulb. Rarely also 9 tentacles observed. Alternating with the tentacles 2-5 small bulbs (max. total 34) with a short, blunt tentacle stump, all the same size and also with a red ocellus. Usually with brown pigment dots in the stomach wall (Fig. 6C, E).

Distribution: Circumglobal in tropical to subtropical waters (Schuchert, 2007). Type locality: Fiji Islands.

16S Data: The partial 16S gene sequence (MW528650) obtained was used to search for similar sequences in GenBank using the blastn function. Other similar sequences found were as expected of Pandeidae species but had only identities below 89%. The similarities with the *Pandeopsis* species described below were also relatively low (<86%, see also Fig. 8).

Remarks: The species has recently been redescribed and discussed by Schuchert (2007), but the problem with the type locality remains unresolved. No type material could be located in the Harvard Museum of Zoology (A. Baldinger, pers. com. June 2019), the museum Agassiz and Mayer were associated with.

Agassiz & Mayer (1899) introduced the name *Pandea violacea* in a paper reporting on medusae collected in the Fiji archipelago. In the description – no figure was given – they state that they have also found indistinguishable medusae at the Dry Tortugas Islands which they intended to illustrate in a subsequent publication. Notwithstanding, the paper dealt with specimens from Fiji and therefore the Fiji Archipelago should be considered as the type locality of the species. This could be taxonomically important if future genetic studies show that the two populations belong to separate species.

In one of our specimens (BFLA4006), some tentacle bulbs had atypical abaxial spurs formed by thickening of the exumbrellar epithelium (Fig. 6B). Several specimens also had brown dots in the stomach wall (Fig. 6A, C). There seem to be differences between Pacific and Atlantic individuals, including the colouration (comp. Bigelow, 1909; or Schuchert, 2020: photos of Australian *Merga violacea*).

Genus *Pandeopsis* Kramp, 1959

Pandeopsis Kramp, 1959b: 39; type species *Pandeopsis scutigera* Kramp, 1959 by original designation.

Diagnosis: Pandeid medusae with wide, large manubrium and quadratic base, with long mesenteries; gonads smooth, sheet-like, covering interradial surface of manubrium, usually with a few dark spots in living or recently fixed specimens; mouth with four simple lips; up to 16 marginal tentacles and up to 24 rudimentary bulbs that may have a very short tentacle stump; tentacular cirri absent; tentacle bulbs without spur, with abaxial ocelli.

Hydroid known only from rearing; colony with common hydrorhiza giving numerous hydranths with one whorl of 3-6 filiform tentacles; medusa buds unknown.

Remarks: The only tangible difference of *Pandeopsis* and *Merga* is the more quadratic stomach base in the former. While some *Pandeopsis* specimens examined here indeed had a wide, quadratic stomach base (Fig. 7C), the difference to *Merga* is not always distinct and both genera could therefore be regarded as congeneric. The 16S phylogenetic tree (Fig. 8) suggests that the two genera are not closely related, but this needs confirmation with additional markers.

Pandeopsis ikarii (Uchida, 1927)

Fig. 7A-C

Tiaranna ikarii Uchida, 1927a: 208: fig. 35.

Pandeopsis ikarii. – Kramp, 1961: 444. – Kramp, 1965: 39, synonymy. – Kramp, 1968: 41, fig. 105. – Schuchert, 1996: 73, fig. 43a-b. – Buecher *et al.*, 2005: 43. – Kubota *et al.*, 2011: 57, figs 1-3. – Suehiro & Kubota, 2015: 73, fig. 1, pl. 1.

Pandeopsis scutigera Kramp, 1959b: 232, fig. 7, Gulf of Thailand. – Kramp, 1961: 113, 444. – Kramp, 1968: 41, synonym.

? not *Pandeopsis ikarii*. – Bouillon, 1980: 336. – Bouillon, 1985: 257, fig. 6, life cycle. [? = *Pandeopsis prolifera* n. spec.]

Examined material: BFLA4088; 1 specimen; 07-MAY-2019; size 2.5 mm, faintly greeninsh gastrodermis, no dots on manubrium seen; preserved in ethanol for DNA extraction; 16S sequence MW528673. – 08-AUG-2018; 1 specimen photographed; size approximately 5 mm, greenish manubrium, dots present; not collected.

MHNG-INVE-0092017; Japan, Mie Prefecture, Toba City; WGS84 34.4781, 136.8670; collector and donor

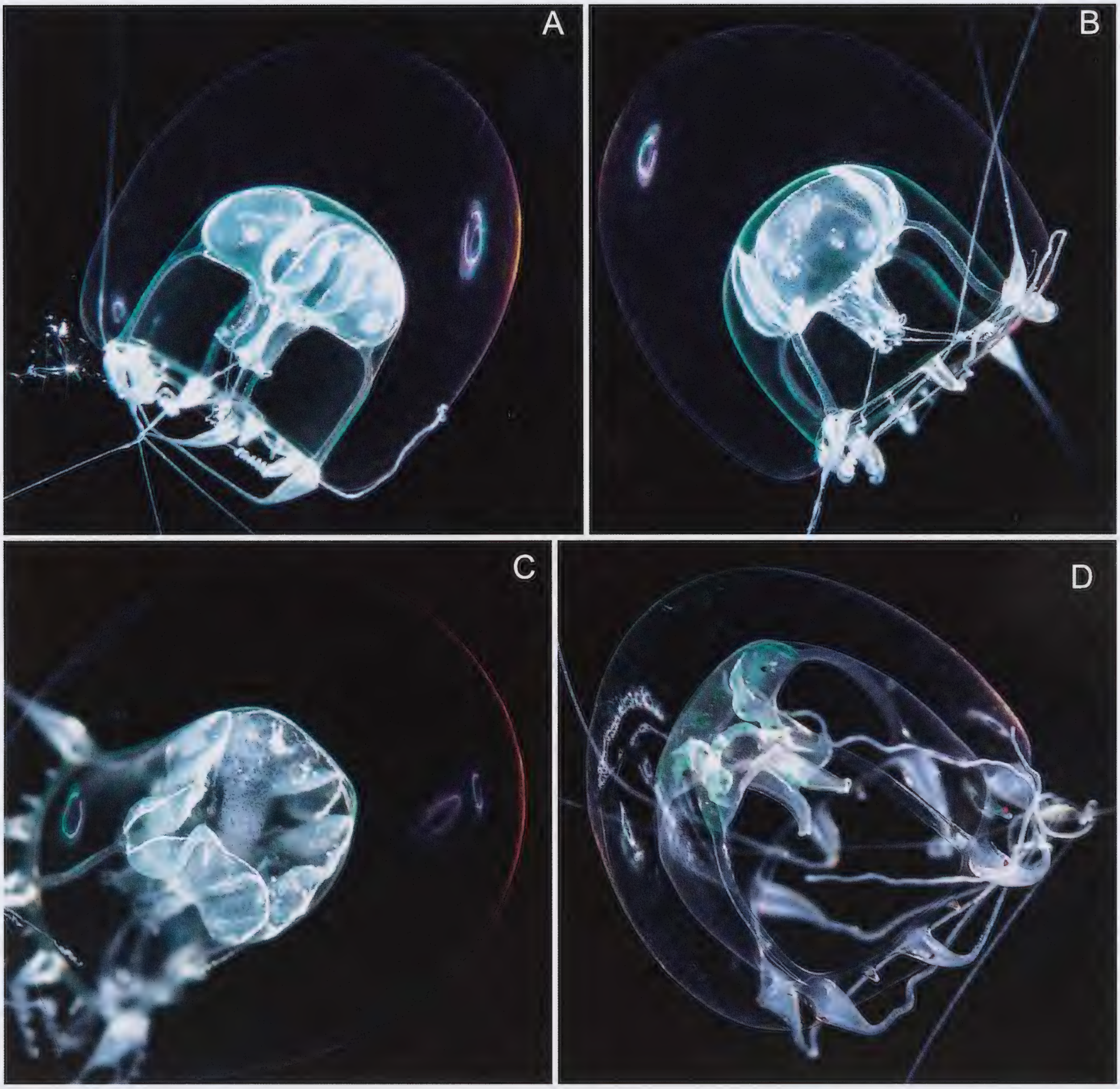


Fig. 7. *Pandeopsis ikarii*. (A-C) Specimen BFLA4088, size 2.5 mm, presumable incipient oocytes are visible in the stomach wall. (D) Specimen collected 08-AUG-2018, size 5 mm, the identification is somewhat unreliable as there is no sequence data available.

Takanori Suehiro; year 2015; 12 medusae cultivated from a polyp stage collected on sand, age about 3 months, examined alive and preserved, size 4 mm, 12 tentacles; 16S sequence MG136757.

Observations: Sample BFLA4088, bell height 2.5 mm, bell top rounded, lower lateral walls straighter, mesogoea thick, at apex nearly 1/2 of bell height, smooth. Manubrium large, base square-shaped, wide upper half, narrower lower part with cross-shaped section, mouth drawn out into four lips with smooth rim; colour greenish, no pigment dots; wall of upper half of manubrium apparently with layer of numerous developing oocytes (Fig. 7A). Radial canals forming mesenteries along upper half of manubrium, smooth, greenish. Eight tentacles, long, tapering, with red abaxial ocellus at base. Eight adradial rudimentary bulbs with a very short, stump-like tentacle, with abaxial red ocellus (Fig. 7B). Individual collected 08-AUG-2018 similar but larger (5 mm), with dots on manubrium (Fig. 7D).

16S Data: An blastn search with the partial 16S gene sequence (MW528673) was used to search for similar sequences in GenBank. The closest match with 3.5 % sequence divergence was with sequence MG136757

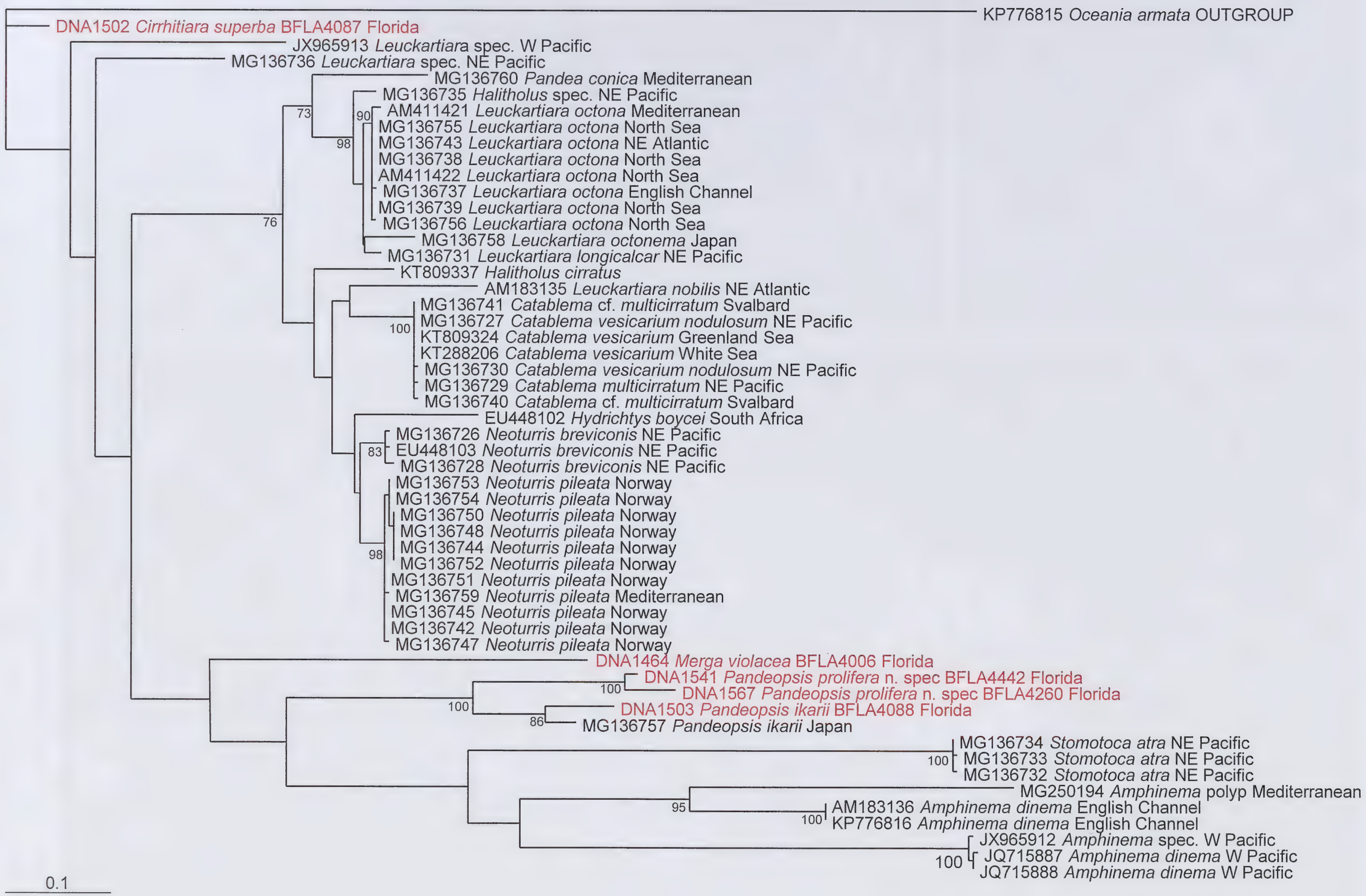


Fig. 8. 16S rRNA maximum likelihood phylogenetic tree of Pandeidae species obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Red labels are new sequences from this study. All sequence labels start with the GenBank numbers permitting the retrieval of more information. For more details see text and Schuchert (2018). Samples based on the polyp stage are indicated, all others are medusa samples.

obtained from a *Pandeopsis ikarii* sample from Japan (see also Fig. 8 and the discussion of the next species).

Distribution: Japan, Philippines, Gulf of Thailand, Java Sea, New Zealand, Indian Ocean, Red Sea. Type locality: Seto (Wakayama), Japan.

Remarks: This is the first record of this species for the Atlantic Ocean. Notably sample BFLA4088 (Fig. 7A-C) matched very well the existing descriptions of this species given above in the synonymy. The only difference being the absence of pigment dots on the stomach wall. They might develop later only (comp. Suehiro & Kubota, 2015). Another observed specimen (Fig. 7D) had such spots, but as no sequence information is available for this specimen the identification remains somewhat uncertain.

Pandeopsis ikarii has been widely reported in the Indian- and Pacific Oceans, but some of these records might belong to a distinct species. Bouillon (1980: 336) observed that his animals from the Bismarck Sea had a dense proliferation of medusa buds on the manubrium and developed up to 14 tentacles. The budding was sometimes already present in young animals with four tentacles only. The maximal size was up to 10 mm, thus quite larger than usually reported (4.5 mm in Kramp, 1968). Another detail mentioned by Bouillon is a band of chordoid cells along the four corners of the manubrium ending in nematocysts clusters, an element neither observed here nor mentioned in other descriptions of the species. The budding was also observed by Navas (1971, cited in Bouillon, 1980) in animals collected in the Indian Ocean, but not by any other observer. Dr Shin Kubota (pers. com.) informed us that he never observed medusa buds in Japanese *P. ikarii*. It is therefore very likely that Bouillon's material belonged to another species, perhaps even *Pandeopsis prolifera* n. spec described below.

Pandeopsis prolifera n. spec.

Fig. 9A-E

Holotype: BFLA4442; collected 07-JUN-2020; size 8 mm; part of specimen preserved in formalin and deposited in Florida Museum of Natural History, catalogue number UF-014057; before formalin fixation, about 1/4 of animal was cut and preserved in ethanol for DNA extraction (MHNG-INVE-0137381); 16S sequence MW528727.

Other examined material: BFLA4260; 1 specimen; 07-MAY-2019; size 5 mm; preserved in ethanol for DNA extraction; 16S sequence MW528695.

Type locality: USA, Florida, 5.5-12 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Diagnosis: *Pandeopsis* medusa with medusa budding on manubrium wall in mature animals, eight tentacles, approximately 24 rudimentary bulbs; stomach base square-shaped in younger animals.

Description: Bell size up to 8 mm, bell higher than wide (Fig. 9A), bullet-shaped, jelly very thick, apical jelly takes up about 1/3 of total height, lateral walls also thick. Exumbrella smooth. Manubrium large, square-shaped base in younger individual, more cross-shaped in older specimen (Fig. 9C); manubrium with wide upper part (stomach) filling nearly half the subumbrella and attached to it via mesenteries, narrower lower part of manubrium with cross-shaped section, mouth drawn out into four lips with slightly undulated rim; manubrium colourless but with pigment dots (Fig. 9D). In holotype interradial stomach wall densely beset with a layer of medusa buds of different developmental stages, about 50 per quadrant, white, in some buds red pigment dots of developing ocelli. Radial canals thick, smooth. Eight tentacles, long, tapering, not much laterally compressed, with red abaxial ocellus at base. 24 adradial rudimentary bulbs with a very short, stump-like tentacle, with abaxial red ocellus (Fig. 9B, D).

16S Data: See Fig. 8, Table 1, and below under Remarks.

Distribution: Type locality only.

Remarks: Our main argument to separate *P. prolifera* from *P. ikarii* is the distinct separation in the phylogenetic analysis (Fig. 8). The observed base pair differences between the two clades were 7.2 to 8.9 %, which is rather large in comparison to the intraspecific variation seen in the other Pandeidae (comp. Fig. 8) but could also be in part due to generally longer branches in this cluster.

However, there are also morphological differences between the animals identified here as *P. prolifera* and *P. ikarii*:

- medusa buds on manubrium (Fig. 9A) versus no buds on manubrium (Fig. 7A-B),
- three rudimentary bulbs between tentacle pairs even in younger medusae (Fig. 9D) versus one only (Fig. 7B),
- colourless manubrium (Fig. 9) versus greenish manubrium (Fig. 7).

We acknowledge that all these differences could be due to a low sample number bias and not fully-grown individuals. More samples could blur the differences and require that both morphotypes be regarded as conspecific. The high intraspecific genetic divergence would be surprising though.

Genus *Larsonia* Boero, Bouillon & Gravili, 1991

Stomotoca (*Stomotocanna*) Haeckel, 1879: 52; type species *Stomotoca pterophylla* Haeckel, 1879 by monotypy.

Larsonia Boero, Bouillon & Gravili, 1991: 198; type species *Stomotoca pterophylla* Haeckel, 1879 by original designation.

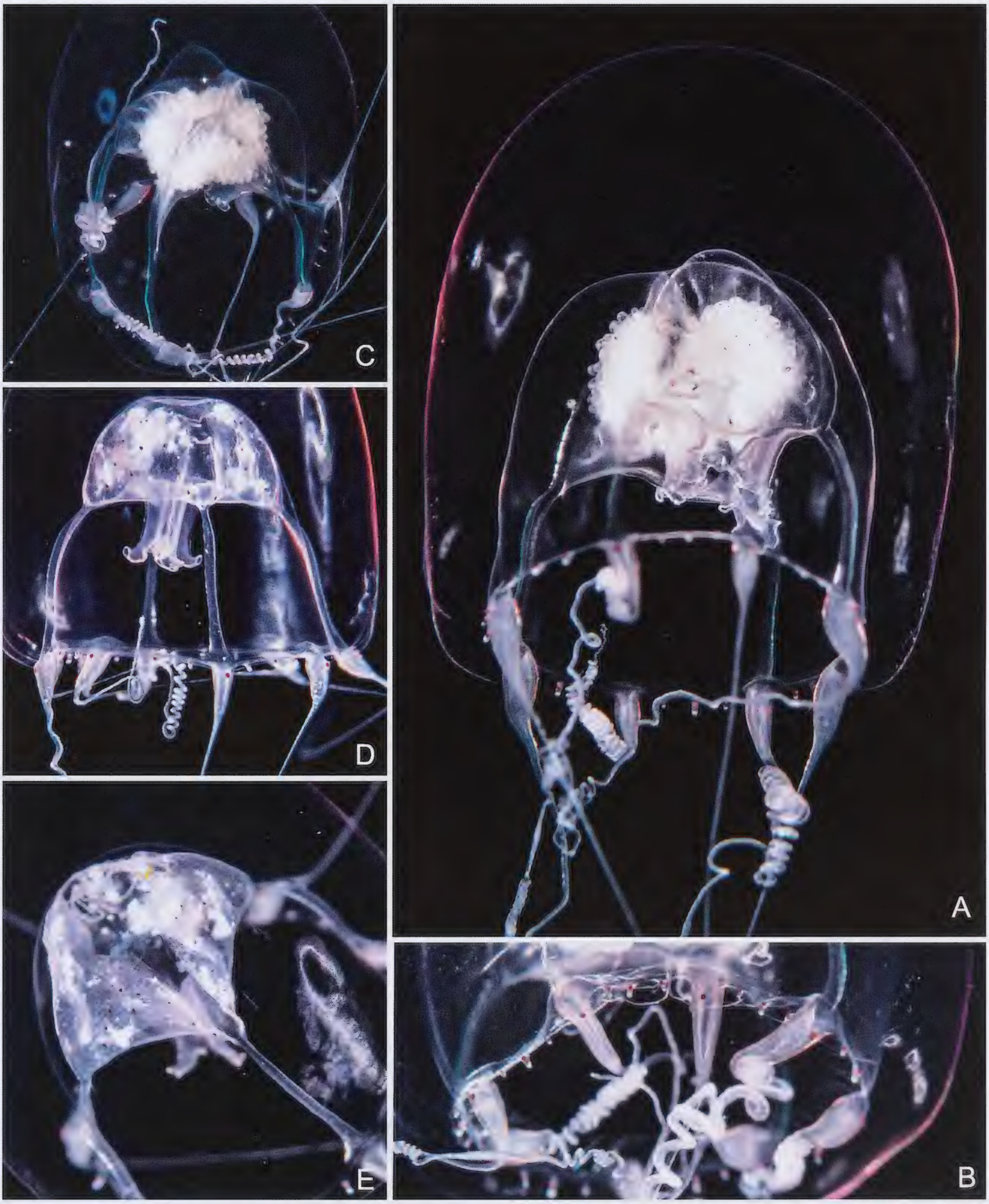


Fig. 9. *Pandeopsis prolifera* n. spec. (A-C) Holotype, BFLA4442, bell height 8 mm. (D-E) BFLA4260, size 5 mm. (A) Lateral view. (B) Bell margin in oral view. (C) Oblique view on aboral part, note shape of manubrium base which is not obviously square-shaped. (D) Lateral view. (E) Oblique view on aboral part, base is square-shaped, some incipient oocytes are visible, food items are in the lumen.

Diagnosis: Medusa with thick apical mesoglea and usually pointed apex; manubrium large, attached to a broad gastric peduncle, extending well beyond bell margin, mouth with crenulated lips; gonads in 8 adradial rows on manubrium, complexly transversely folded; two opposite perradial tentacles, numerous rudimentary bulbs on bell margin; no ocelli.
Hydroid parasitic on fish, with plate-like naked hydrorhiza, hydranth with no tentacles; gonozooid branched, producing at ends medusa buds.

Remarks: Larson (1982) reared medusae released from a parasitic hydroid of the genus *Hydrichthys* Fewkes, 1887 and could identify them as *Stomotoca pterophylla* Haeckel, 1879. Because Larson's hydroid showed little host specificity and many *Hydrichthys* polyps are rather similar, Larson concluded that they will also produce medusae referable to the genus *Stomotoca* L. Agassiz, 1862. Therefore, he suggested to synonymize *Hydrichthys* and *Stomotoca*. This was contested by Boero & Bouillon (1989) who could show that the type species of *Stomotoca – S. atra* L. Agassiz, 1862 – had a polyp stage that was completely different from *Hydrichthys* (free living, with scattered tentacles). Moreover, the polyp of a tentatively identified *Hydrichthys mirus* Fewkes, 1887 – type species of the genus *Hydrichthys* – produced a *Leuckartiara*-like medusa (Boero *et al.*, 1991). Because *Stomotoca pterophylla* and *Stomotoca atra* have different polyps, Boero *et al.* (1991) proposed the new genus *Larsonia* for *S. pterophylla*. Boero *et al.* must have overlooked that Haeckel (1879) had already introduced a subgenus name for *S. pterophylla*, namely *Stomotocanna* Haeckel, 1879. As a subgenus level name automatically also becomes available at the genus level, *Larsonia* Boero, Bouillon & Gravili, 1991 is a junior synonym of *Stomotocanna*. However, because Haeckel's name has not been used since its introduction and in the interest of nomenclatural stability, it should not be reactivated (ICZN, paragraph 23.9.1.1.)

***Larsonia pterophylla* (Haeckel, 1879)**
Fig. 10A-D

Stomotoca (Stomotocanna) pterophylla Haeckel, 1879: 52, pl. 4 fig. 10.
Stomotoca pterophylla.– Mayer, 1910: 113, pl. 29 figs 3-5, pl. 30 fig. 7. – Bigelow, 1918: 372, synonymy, discussion of species. – Uchida, 1940: 284, fig. 3. – Kramp, 1959a: 119, fig. 115. – Kramp, 1961: 115. – Kramp, 1968: 44, fig. 113. – Larson, 1982: 433, fig. 183. – Wedler & Larson, 1986: 97, fig. 11a-b, hydroid, young medusa.
Stomotoca divisa Maas, 1897: 11, pl. 1 figs 1-9. – Vanhöffen, 1913b: 14, synonym.
Larsonia pterophylla. – Boero *et al.*, 1991: 198, new combination. – Woodstock *et al.,* 2019: fig. 1, hydroid.
Stomotoca atra. – Vanhöffen, 1913b: 14, pl. 2 figs 12-16. – Stampar & Kodja, 2007: 55, figs 2-3. [not *Stomotoca atra* L. Agassiz, 1862]

Examined material: BFLA4453; one formalin fixed specimen deposited under catalogue number FU-014064; collected 08-JUN-2020; height 27 mm. – 08-AUG-2018, 1 specimen photographed; not collected...

Observations: Medusa 27 mm, with low umbrella and big, conical, pointed apical process; subumbrella shallow; with broad gastric peduncle reaching to velum level; 4-5 ribbon-like radial canals; two opposite tentacles, long, whitish, with swollen base clasping bell margin, no ocelli; about 80-100 atentaculate bulbs along bell margin, small, wart-like, all about the same size, without ocelli (Fig. 10C); manubrium barrel-shaped, with mouth drawn out into four long perradial lips, margin crenulated; gonads large, covering stomach in eight adradial series of about 10 branched folds directed towards interradial, pairs of adradial fold series connected perradially by a thick, vertical fold; adradial folds branching with up to four ends (Fig. 10B). Gonads and manubrium colour golden-brown or brown.

Distribution: American coasts from Gulf of Maine to Brazil, West Africa, Pacific coasts of Panama to Peru, Japan, Papua New Guinea, Indian Ocean (Kramp, 1968; Bouillon, 1980; Navas-Pereira & Vannucci, 1991; Stampar & Kodja, 2007, as *Stomotoca atra*). Type Locality: Caribbean Sea, 20.60°N 79.00°W.

Remarks: The observed specimens agreed well with existing descriptions of *Larsonia pterophylla*, except that one had five radial canals instead of four. This surplus radial canal was interpreted as a developmental aberration or variation without taxonomic significance. Also other tetraradial hydromedusa species occasionally show three or five radial canals (see *Clytia* spec.).
Stomotoca atra L. Agassiz, 1862 is a very similar species and Vanhöffen (1913b) thought that they could be conspecific. However, *S. atra* is distinct from *L. pterophylla*, notably they have different polyp stages (comp. Larson, 1982 and Boero & Bouillon, 1989). The medusae are distinguishable: in *L. pterophylla* the mouth margin is crenulated and perradially drawn out into long lips, in *S. atra* it is not crenulated and the perradial lips are short. Additionally, the transverse gonad folds are branched several times in *L. pterophylla*, while they are mostly unbranched in *S. atra* (comp. Schuchert, 2017b) or in loops in very mature animals (comp. Bigelow, 1918; Arai & Brinckmann-Voss, 1980). The Brazilian medusae depicted in Stampar & Kodja (2007) and identified as *S. atra* must thus belong to *L. pterophylla*.

Family Oceaniidae Eschscholtz, 1829
Genus *Turritopsis* McCrady, 1857

Synonymy: See Schuchert (2020).

Diagnosis: Medusae with high bell, proximal portion of radial canals swollen through vacuolated gastrodermal

Fig. 10. *Larsonia pterophylla.* (A) BFLA4453, lateral view of animal, size 27 mm. (B) BFLA4453, close up of manubrium in lateral view. (C) Animal photographed 08-AUG-20181 part of bell margin in aboral view showing rudimentary tentacle bulbs (warts).

cells, forming a peduncle-like mass on top of manubrium, in larger animals continued on manubrium as perradial ribs. Tentacles numerous and evenly distributed. Mouth four-lipped, fringed with numerous spherical nematocyst clusters, these with or without a distinct stalk. Ocelli adaxial on tentacle base.

Polyp stage forming erect, branching colonies, side-branches and hydranth pedicels adnate for some distance, perisarc tubes not nested. Hydranths spindle- to club-shaped; filiform tentacles scattered over much of hydranth body. Gonophores develop on the hydrocauli in perisarc covered region and are liberated as medusae.

Remarks: The genera *Turritopsis* McCrady, 1857 and *Oceania* Péron & Lesueur, 1810 are morphologically not separable (comp. Schuchert, 2016). The purported difference of the stalked oral nematocyst buttons in *Oceania* is not tenable as also *T. nutricula* has stalked clusters (see below). However, to avoid unnecessary taxonomic changes, the two genera should not be synonymized until a comprehensive molecular phylogeny using several marker genes confirms this.

Turritopsis nutricula McCrady, 1857

Fig. 11A-D

Oceania (Turritopsis) nutricula McCrady, 1957: 55, pl. 4 figs 1-10.

Turritopsis nutricula. – Brooks, 1883: 465. – Brooks, 1886: 388, pl. 37. – Brooks & Rittenhouse, 1907: 429, pls 30-35, development. – Mayer, 1910: 143, figs 10-13, pls 14-15. – Goy, 1979: 270, fig. 4. – Wedler & Larson, 1986: 86, fig. 5B. – Schuchert, 2004: 327, figs 2A-B, 3D-E, revision. – Miglietta *et al.,* 2018a: fig. 2. – Calder, 2019: 12, fig. 1e.

Modeeria multitentaculata Fewkes, 1881: 149, pl. 3 figs 7-9.

Examined material: BFLA4391; 1 specimen; 17-MAY-2020; size 3 mm; preserved in alcohol for DNA extraction; 16S sequence MW528718. – BFLA4416; 1 specimen; 28-May-2020; size 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528724.

Observations: Typical *Turritopsis* medusae, bell heights up to 3 mm, manubrium yellow, blocks of vacuolated cells at manubrium base with deep interradial clefts, thus clearly separated (Fig. 11B-C), tentacle numbers about 50, base with an adaxial ocellus, tentacle tips swollen in life. Nematocyst buttons lining the mouth margin with stalks like in *Oceania armata*.

16S Data: The two 16S sequences obtained had only 0.5% base pair divergence. In order to compare them

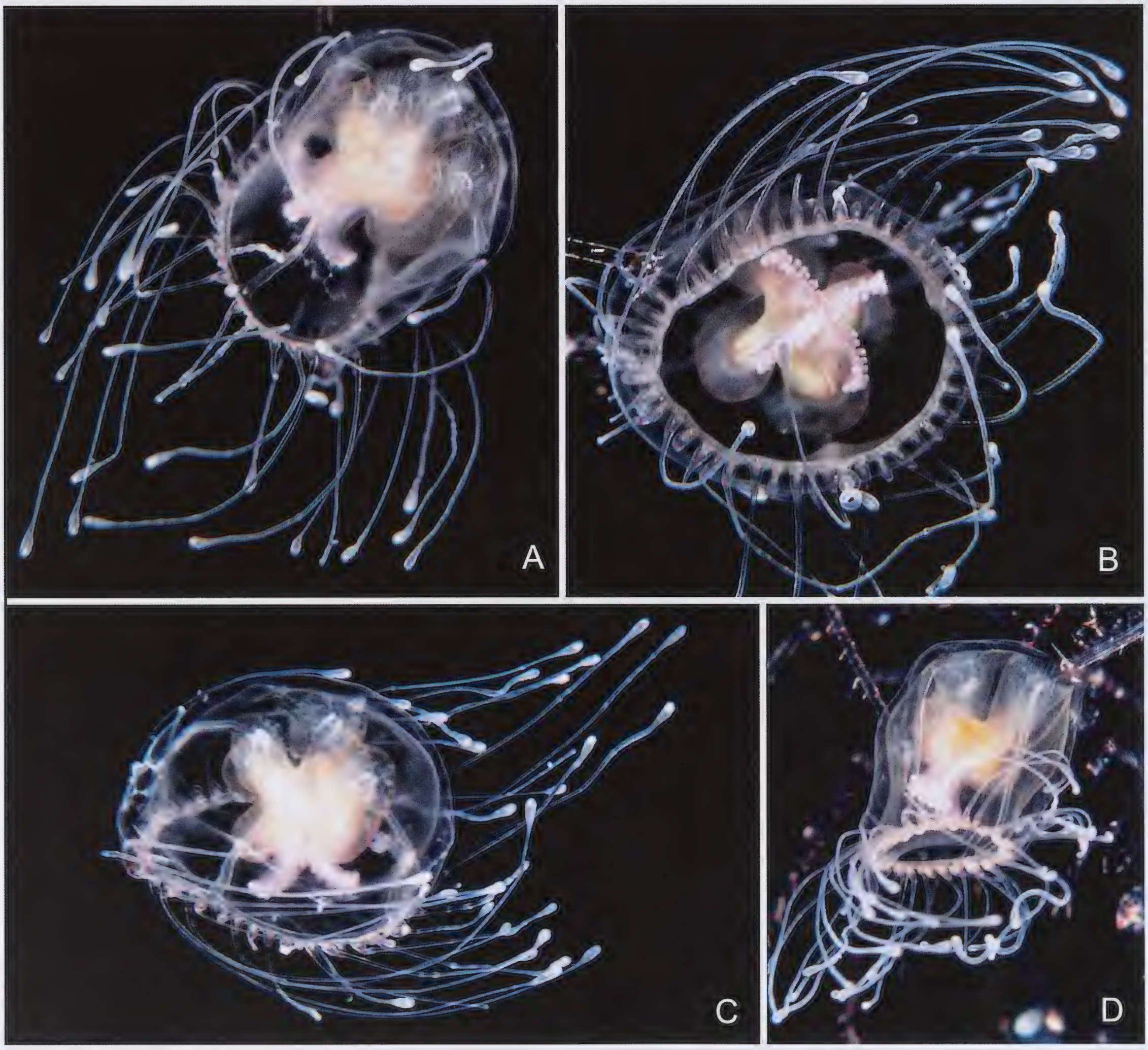


Fig. 11. *Turritopsis nutricula*. (A-C) Specimen BFLA4416, bell height 2 mm. (D) Specimen BFLA4416, 3 mm height. (A) Oblique view of animal. (B) Oral view, note nematocyst clusters along mouth margin and the interradially separated blocks of vacuolated cells at manubrium base. (C) Oblique view. (D) Lateral view, in the background some appendages of a decapod.

to other existing sequences, they were added to the set of sequences used in Miglietta *et al.* (2018a) and a maximum likelihood phylogenetic analysis was made (results not shown). Both sequences of this study clustered with sequences of *T. nutricula* from Woods Hole (GenBank numbers EU624349 and EU624348) and others from Panama (e.g. EU62435), thus fall within the clade of *T. nutricula* of Miglietta *et al.* (2018a).

Distribution: Temperate to tropical coastal regions of the western Atlantic Ocean from Woods Hole to Brazil, Gulf of Mexico, Caribbean Sea. Type locality: Atlantic Ocean, USA, South Carolina, Charleston Harbor.

Remarks: The samples examined here matched unambiguously *Turritopsis nutricula* in the restricted sense of Schuchert (2004). The yellow manubrium and particularly the interradially split blocks of vacuolated cells at the manubrium base are diagnostic for *Turritopsis* medusae of this region. Moreover, the sampling site is in the same biogeographic region as the type locality, the latter being about 800 km away. There can thus be little doubt that these specimens represent the true *T. nutricula*.

Species delimitation in the genus *Turritopsis* was difficult and until the revision of Schuchert (2004) most authors assumed that there is only a single, circum-globally occurring species named *T. nutricula*. Schuchert (2004) using morphological data showed that this is not the case and re-established several previously synonymized names. This was then later confirmed using genetic data [see summary in Miglietta *et al.* (2018a) and references therein]. However, so far it was not clear which of the molecular clades corresponded to the true *T. nutricula*. Although the studies of Miglietta *et al.* included specimens identified as *T. nutricula*, their identity was uncertain because they were either based on young medusae or polyps. Both of them are not unambiguously identifiable. The results of the present study confirm the correct identification of the *T. nutricula* clade in Miglietta *et al.* (2018a).

Family Bythotiaridae Maas, 1905
Genus *Protiaropsis* Stechow, 1919

Heterotiara Maas, 1905: 19, invalid junior homonym of *Heterotiara* Pomel, 1883 (Echinodermata).

Protiaropsis Stechow, 1919: 150, nom. nov. pro *Heterotiara* Maas, 1905, type species *Heterotiara anonyma* Maas, 1905 by original designation.

? *Kanaka* Uchida, 1947: 304, type species *Kanaka pelagica* Uchida, 1947 by monotypy.

? *Gymnogonium* Xu & Huang, 1994: 152, type species *Gymnogonium zhengzhongii* Xu & Huang, 1994 by original designation.

Diagnosis: Bythotiaridae medusae with thick umbrella, four simple radial canals; no centripetal canals; gonads interradial, no transverse folds; no secondary tentacles; no ocelli. Hydroid unknown.

Remarks: For a key to the currently known species see Du *et al.* (2018).

Protiaropsis anonyma (Maas, 1905)
Fig. 12 A-C

Heterotiara anonyma Maas, 1905: 19, pl. 3 figs 19-21. – Bigelow, 1909: 216, pl. 41 figs 12-14. – Vanhöffen, 1911: 211, pls 12-13. – Bigelow, 1918: 382. – Bigelow, 1928: 287. – Russell, 1940: 516, figs 5-7. – Kramp, 1959a: 17, 125, fig. 131. – Kramp, 1961: 122. – Kramp, 1965: 41. – Kramp, 1968: 53, fig. 138. – Schmidt, 1973: 22. – Schmidt & Klinker, 1974: 34. – Bouillon, 1980: 314. – Brinckmann-Voss & Arai, 1989: 41, figs 1b, 1e.

not *Heterotiara anonyma.* – Bigelow, 1913: 25, records North Pacific. [= *Bythotiara depressa* Naumov, 1960]

in part *Heterotiara anonyma.* – Arai & Brinckmann-Voss, 1980: 69, fig. 40. [in part *Bythotiara depressa* Naumov, 1960]

Protiaropsis anonyma. – Stechow, 1919: 150, new combination. – Schuchert, 2010: 338.

? *Kanaka pelagica* Uchida, 1947: 103, fig. 5. – Kramp, 1961: 123. – Kramp, 1968: 58, fig. 153. – Schmidt, 1973: 22, could be a young *Heterotiara anonyma*. – Bouillon, 1980: 316, could be *Heterotiara anonyma*.

Examined material: BFLA4037; 1 specimen; 26-MAR-2019; size 12 mm high; part preserved in formalin and deposited as UF-013457, small part in alcohol for DNA extraction; 16S sequence MW528657.

Observations: Bythotiaridae medusa 12 mm high, bell cylindrical, not compressed laterally, mesoglea thick, especially apical jelly which is about 1/3 of the total bell height; bell margin with regular furrows in which lie the tentacles. Manubrium 2/3 the height of the subumbrella, shaped like inverted cone, section cross-shaped, interradial wall smooth, mouth cruciform, rather small, four red strands run along the interradial corners of the manubrium. Four thin radial canals, no mesenteries; circular canal thin. 10 tentacles, length about half the height of the bell, originating from under circular canals without formation of a distinct tentacle bulb but with an epidermal swelling at the junction of tentacle and circular canal, proximal part of tentacles curving adnate around bell margin in furrows, tapering only slightly distally, ending in bright orange, spherical to ovoid knob, diameter about 0.3 mm. No ocelli.

16S Data: A blastn search in GenBank with the sole 16S (MW528657) gave mostly species of Filifera/Anthoathecata, but all below 90% identity and thus precluding any conclusions on relationships.

Distribution: Widespread in warm parts of the Atlantic, Indian, and Pacific Oceans, usually in depths of 0 to 600 m (Arai & Brinckmann-Voss, 1980; corrections in Brinckmann-Voss & Arai, 1989). Type locality: Indonesia, 0.2933°S, 129.2418°E, 0-1000 m depth.

Fig. 12. *Protiaropsis anonyma,* specimen BFLA4037, bell height 12 mm. (A) Lateral view of animal with amphipod prey in its stomach. (B) Manubrium at other angle, note cruciform base. (C) Bell margin.

Remarks: Most illustrations of this species do not show the terminal swellings of the tentacles (e.g. in Kramp, 1959a, 1968), a typical character of Bythotiaridae medusae. These are almost invariably lost in specimens caught with a plankton net, but they are normally present in this species (see Kramp, 1948, 1965; Schmidt, 1973; Arai & Brinckmann-Voss, 1980).
The size of the examined medusa was at the lower end of the range usually given for this species (12-20 mm, Maas, 1905; Bigelow, 1909; Vanhöffen, 1911). Bigelow (1918) also found somewhat smaller (up to 13 mm) in the nearby Bermuda region, likewise Bouillon (1980) in animals from Papua New Guinea.
The interradial red strands are rather conspicuous in the living and preserved animal (Fig. 12A-B), but they have been mentioned only rarely so far. Only Vanhöffen (1911) observed them in an animal caught near the Nias Islands (Indonesia).
The nematocysts have been described by Russell (1940) and Bouillon *et al.* (1988a). The species has large desmonemes which are typical for the family Bythotiaridae.
The taxonomic scope of *Protiaropsis anonyma* is not yet fully clear as there are other similar species, some of which which could prove to be conspecific (see also discussions in Schmidt, 1973).
Protiaropsis minor (Vanhöffen, 1911) is somewhat smaller (6-12 mm), has perhaps a shorter manubrium, and 16 to 24 tentacles (see description by Pagès *et al.*, 1992). Bouillon *et al.* (1988a) found both morphotypes in sympatry and kept them distinct.
Kanaka pelagica Uchida, 1947 has eight tentacles but is much smaller (1.8 mm). It was based on a single specimen which was likely a juvenile. Kramp (1953) thought it might belong to *P. minor*, while Schmidt (1973) and Bouillon (1980) think it is referrable to *Protiaropsis anonyma*.
Gymnogonium zhengzhongii Xu & Huang, 1994, is small (2.2 mm), has a short manubrium, and a pair of branched radial canals, resulting in six canals in total. The manubrium of the only observed specimen had gonads. Bouillon *et al.* (2006: 182) thought that it could belong to *Protiaropsis anonyma*. As the the species is based on a single specimen, it cannot be excluded that the branched radial canals were a developmental aberration. New material has to prove the validity of the species, but as the type specimen was apparently mature at 2.2 mm, the genus and species should be retained as valid for the moment.
Bouillon (1980) thought that also *Bythotiara depressa* Naumov, 1960 could be conspecific with *P. anonyma* as he found intermediate forms. *Bythotiara depressa* differs from *P. anonyma* in having an irregularly folded surface of the gonads. Brinckmann-Voss & Arai (1989) examined the problem in detail and they worked out diagnostic differences of the two species (see also Xu *et al.*, 2016). Some of the previous records of *P. anyonyma* from colder waters of the North Pacific Ocean were actually *B. depressa*.
All these ambiguities underline the need for a comprehensive dataset of 16S DNA barcodes which will hopefully improve the species delimitations.

Family Ptilocodiidae Coward, 1909
Genus *Thecocodium* Bouillon, 1967

Thecocodium Bouillon, 1967: 1119; type species *Thecocodium brieni* Bouillon, 1967 by original designation.

Diagnosis: Medusa with lobed bell margin, with marginal nematocyst ring from which usually arise several centripetal nematocyst bands or exumbrellar rows of refringent spots. Four radial canals and hollow circular canal, short mesenteries. Four marginal tentacles with bases embedded in umbrellar furrows, no ocelli. Manubrium with short, perradial lips ending in nematocyst clusters; gonads interradial on manubrium.
Hydroid with reticulate, tubular hydrorhiza, covered by perisarc. Polyps on stolons, sessile, naked, polymorphic, usually with gastro-gonozooids and dactylozooids. Gastro-gonozooids cylindrical or club-shaped, without tentacles, hypostome with nematocysts. Dactylozooids thin, solid gastrodermis, terminal group of capitate tentacles. Gonophores fixed sporosacs or free medusae developing in a single whorl on gonozooids. Cnidome of polyp includes desmonemes.

Thecocodium quadratum (Werner, 1965)
Fig. 13A-B

Ptilocodium quadratum Werner, 1965: 11, figs 4-5. – Werner, 1984: 139, fig. 85.
Thecocodium quadratum. – Jarms, 1987: 59, fig. 8.1-8.4. – Kubota, 1993: 89, fig. 1. – Akiyama *et al.,* 2013: 113, figs 1-2.
Thecocodium aff. *quadratum*. – Kubota *et al*., 2018: 7, fig. 2A-B.
Thecocodium spec. – Kubota & Meldonian, 2016: 77, fig. 1.

Examined material: 21-JUL-2018, 1 specimen photographed; not collected. – BFLA4461; 1 specimen; 13-JUN-2020; size 5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528730. – BFLA4466; 1 specimen; 13-JUN-2020; size 4 mm; preserved in alcohol for DNA extraction; 16S sequence MW528731. MHNG-INVE-0039477; schizoholotype, polyps obtained from original culture of Werner (courtesy Dr G. Jarms), origin of material Kenya; cultivated and reared medusae, preserved in Feb-2006; 16 sequence FN422379.

Observations: Medusa with bell-shaped umbrella, up to 5 mm, mesoglea thick, including lateral walls, height of apical jelly at least 1/3 of total height, not delimited as apical process. Bell margin with deep perradial clefts continued as canal-like furrows to mid-

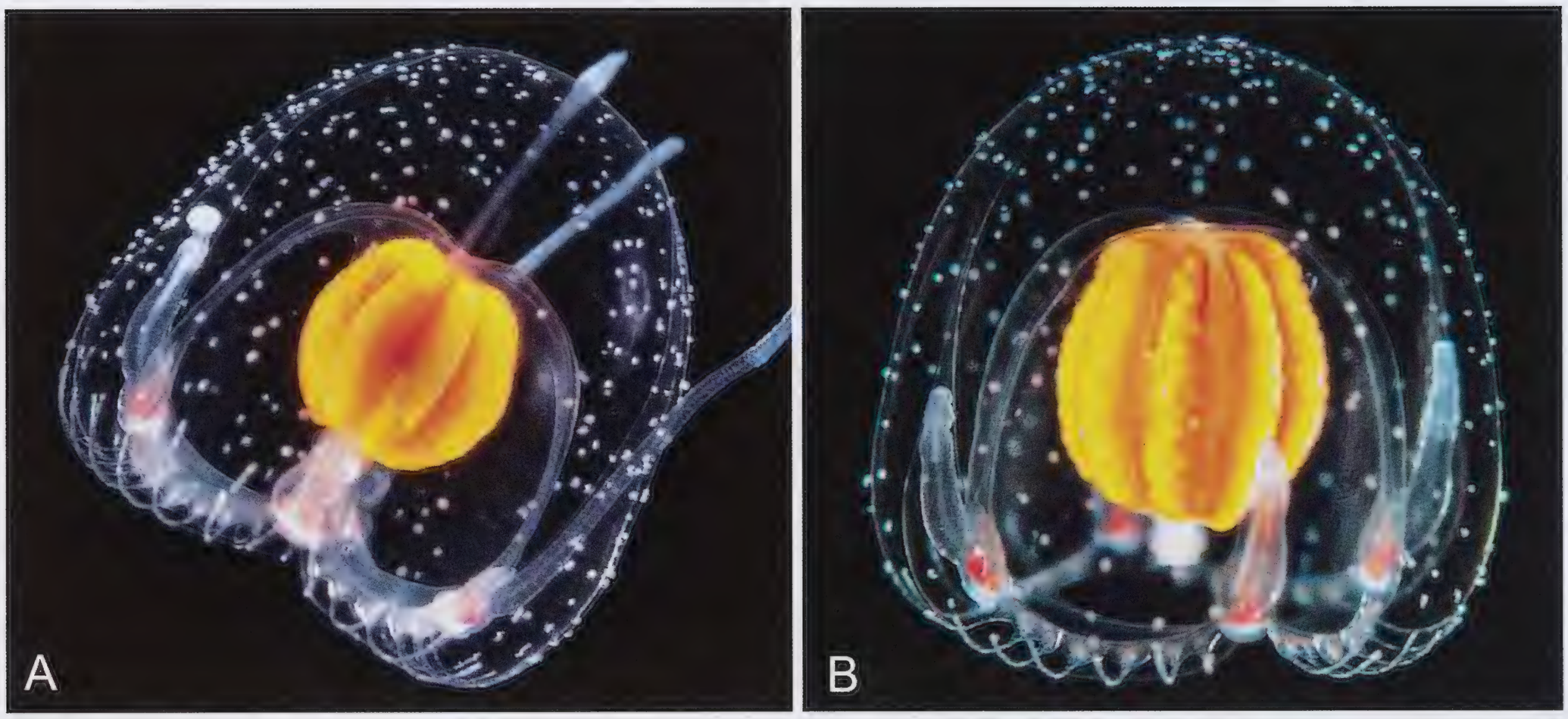


Fig. 13. *Thecocodium quadratum*, females. (A) Specimen photographed 21-JUL-2018. Lateral view of whole animal. (B) BFLA4461, an apparently fully mature female.

height of bell and housing tentacle. Bell margin appears lobed through the clefts, between the furrows on each lobe 5-7 meridional nematocyst tracks originating from near circular canal and curving around bell margin to exumbrella and then dissolving into arrays a few isolated nematocysts clusters, >100 additional nematocyst buttons scattered on entire exumbrella. Four smooth radial canals widened to funnels at the junction to the manubrium. Four tentacles, directed upwards, lying in the canal-like exumbrellar furrows, usually contracted to length shorter than bell height, but able to extend to length at least >3 times the bell height. Tentacles at origin with a small bulb with a pink to red colour, bulb adnate to exumbrella; main trunk of tentacles appears chordoid and is transparent, tapering to tip which is whitish-opaque and sometimes slightly swollen. Manubrium large, with a spherical stomach and a small neck-like oral region, small cruciform mouth; gonads much developed surrounding the manubrium entirely, with a brilliant, intense yellow-orange colour, subdivided in 8 adradial, vertical bulges (Fig. 13B), the whole appearing like a peeled orange composed of 8 wedges, perradial and interradial clefts deep. Females with > 200 eggs.

Distribution: Coast of Kenya (Jarms, 1987); Japan (Kubota, 1993); Taiwan (Kubota *et al*., 2018); Florida (Kubota & Meldonian, 2016; this study). Type locality: Indian Ocean, NE of Mombasa (hydroid, substrate unknown).

16S Data: The two obtained 16S haplotypes differed in 0.5% of their base pairs, the divergences to the type material were 4.3 to 4.5% (Table 1).

Remarks: The descriptions of this species (Werner, 1965; Jarms, 1987) were based on a cultivated hydroid colony and its released medusae reared to subadult stage. It was therefore with some hesitations that subsequent findings of the medusa in the plankton where attributed to this species or they were even only identified to genus level (see synonymy above). The observed specimen from Florida differed from the type material in having a slightly higher umbrella and many more exumbrellar nematocysts clusters. Moreover, the gonads are much more developed. The species has been recorded from Florida waters before (Kubota & Meldonian, 2016). Like Kubota & Meldonian (2016) we are also aware that the identification of the Florida specimens as *Thecocodium quadratum* is to some degree questionable for biogeographic reasons. However, comparing our photos with a medusa from Taiwan published by Kubota *et al*. (2018) it is evident that there are no taxonomically significant differences and this morphotype has likely a very widespread distribution. The 16S sequences from the Florida specimens differed about in 4.5% of the base pairs compared to the type specimen (Table 1). In comparison with other medusae this appears to us as intermediate between intraspecific or interspecific variation, but these few samples and just one marker alone cannot provide conclusive information. Because the morphology of Pacific and Atlantic medusae match, we think it should be attributed to *T. quadratum* until more detailed genetic data prove the contrary.

Family Proboscidactylidae Hand & Hendrickson, 1950

Genus *Proboscidactyla* Brandt, 1835

Synonymy: See Schuchert (2009).

Diagnosis: Medusa umbrella mostly hemispherical; with exumbrellar nematocyst patches or linear arrays of patches alternating with tentacles; radial canals branched; usually instead of circular canal a solid gastrodermal marginal strand; manubrium base with four, six or more radial gastric pouches, extending along proximal portions of radial canals, pouches in some species inconspicuous; gonads surrounding manubrium and extending onto gastric pouches; tentacles with swollen hollow base connected to the lumen of radial canals.

Hydroid on rims of sabellid polychaete tubes, with creeping, naked stolons; hydranths almost sessile, polymorphic; gastrozooid with rounded hypostome, separated from body by a constriction; hypostome with large pad of nematocysts somewhat displaced onto one side, two filiform tentacles arising close together beneath hypostomial constriction and opposite to nematocyst cluster; gonozooids and dactylozooids without tentacles, mouth-less and smaller than gastrozooids; medusa buds close to gonozooid tip.

Remarks: Species delimitation in this genus has a long history of discussions and especially the status of the various variants of *P. ornata* are unclear [comp. Schuchert (2009) and references therein]. The medusae of *P. ornata* are quite variable and a number of species and subspecies have been proposed, mainly based on the presence and position of vegetative medusa buds. Kramp (1957, 1965) examined numerous specimens and concluded that these variants likely belong to the same species, the number of canal ramifications and the place of medusa budding being variable even within the same population.

However, as seen in other medusa-based species – e.g. *Clytia* or *Zanclea* – once also the polyp stage is considered, many morphospecies can sometimes be distinguished (for *Zanclea* see e.g. Boero *et al.*, 2000). Hand (1954), using complete data of the medusa and polyp stage of Pacific *Proboscidactyla* species as well as host data of the polyp colony, found that they differ in minute details. This makes it likely that other widely distributed *Proboscidactyla* species which are solely based on the medusa stage could represent species complexes. DNA sequence results obtained in this study indeed indicate that this seems to be the case for at least *P. ornata*.

Proboscidactyla ornata (McCrady, 1859)

Fig. 14A-G

Willsia ornata McCrady, 1859: 149, pl. 9 figs 9-11.
Proboscidactyla ornata. – Mayer, 1910: 189, pl. 20 figs 1-10, text fig. 100.

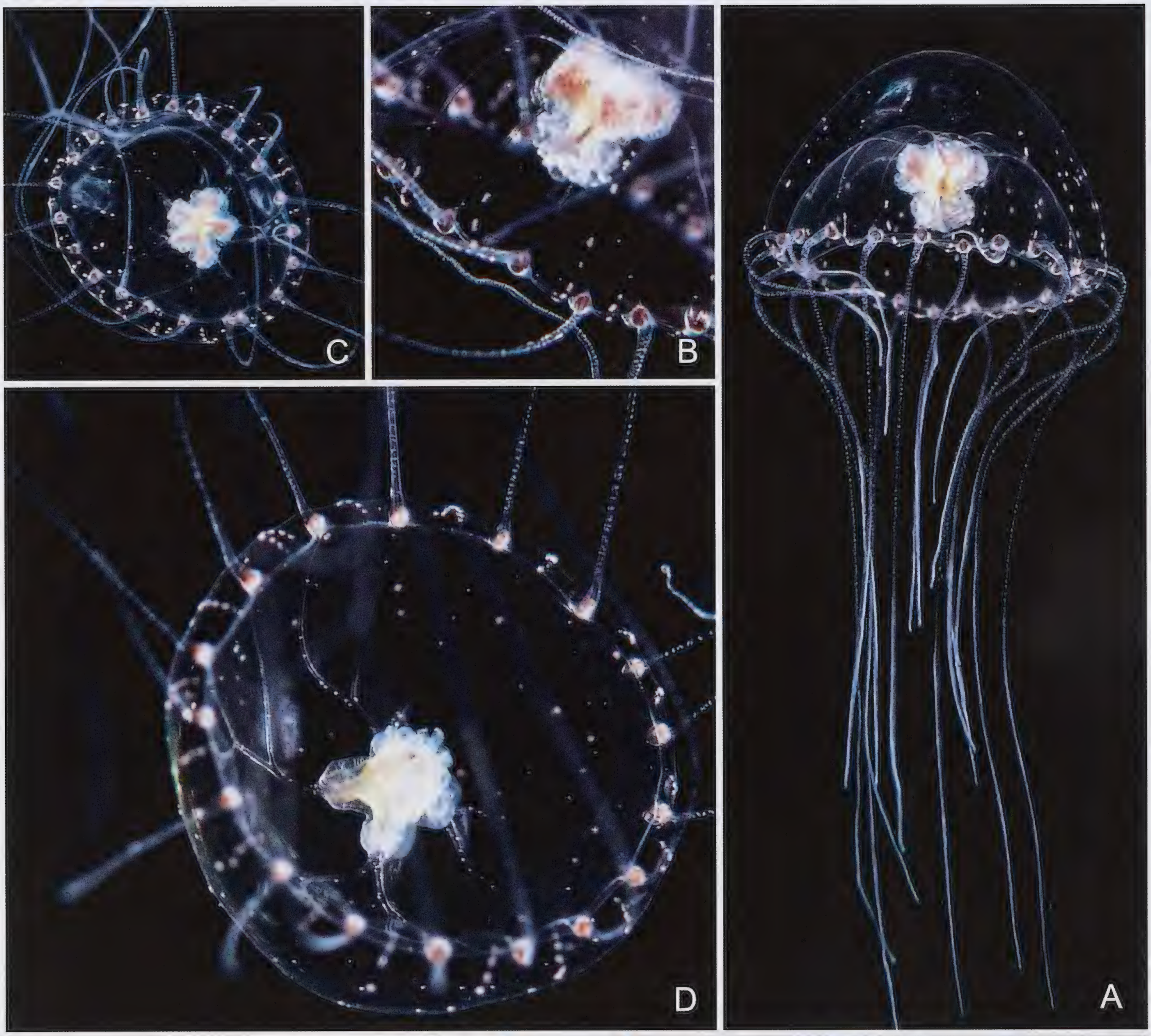
Material examined: BFLA4349; 1 specimen; 11-MAR-2020; size 4 mm, 17 tentacles, presumably a mature male; preserved in alcohol for DNA extraction; 16S sequence MW528709. – BFLA4354; 1 specimen; 11-MAR-2020; size 4 mm, 18 tentacles, with green subumbrella; preserved in alcohol for DNA extraction; 16S sequence MW528710. – BFLA4356; 1 specimen; 13-MAR-2020; size 4 mm, 21 tentacles, mature male; preserved in alcohol for DNA extraction; 16S sequence MW528711. – BFLA4357; 1 specimen; 13-MAR-2020; size 5 mm, 21 tentacles, mature female; preserved in alcohol for DNA extraction; 16S sequence MW528712 – BFLA4454; 1 specimen; 11-JUN-2020; size 5 mm, 19 tentacles; preserved in formalin and deposited as FU-014065. – BFLA4455; 1 specimen; 11-JUN-2020; size 6 mm, 18 tentacles, mature male; preserved in formalin and deposited as FU-014066. – 13-MAR-2020; 1 specimen photographed, not collected; 4 mm, 16 tentacles.

Observations: Medusae with the characteristics of the genus, bell as wide as high, 4-6 mm, apical jelly about 1/3 of total height. Exumbrella with more or less linear arrays of nematocyst patches of variable length, starting from bell margin and alternating with tentacles, some reaching beyond mid part of bell, patches with up to 10 nematocysts, patches often lost in preserved animals. Manubrium rather broad, cruciform base giving impression of four (rarely 5) peradial basal pouches, gonads covering entire interradial wall of stomach, separated perradially, smooth surface; mouth rim much folded but not clearly with four lips, rim with nematocysts. Four (rarely 5) thin radial canals originate from basal manubrium pouches, branching dichotomously so that 4 to 5 ends reach circular canal (= solid strand). Tentacles only at ends of radial canals, 16-21 in mature animals, oviform basal bulb, tapering in much extensible tentacles; abaxial side of bulb gastrodermis with a dark pigment, lost in formalin preserved animals.

16S Data: See Table 1 and Fig. 16. The sequences of this study were quite divergent from *P. ornata* sequences from other regions, showing p-distances of up 7.5% and separating into distinct mitochondrial lineages. The lineage of Florida *Proboscidactyla ornata* without medusa buds is also clearly different from those here identified as *P. gemmifera* (see below).

Distribution: Reportedly circumglobal in tropical and temperate waters, but in view of the genetic data presented below, the known distribution must be restricted to the coastal waters of the NE Atlantic. Type locality: USA, South Carolina, Charleston Harbor.

Remarks: The present material (Fig. 14) agreed well with the descriptions given in McCrady (1859) and Mayer (1910) who had material from the same biogeographic region (warm temperate and tropical northwestern Atlantic; Spalding *et al.*, 2007). The observed differences concerned the tentacle numbers which were 16 to 21, thus more variable than the 16 given in Mayer (1910). Our material observed in situ



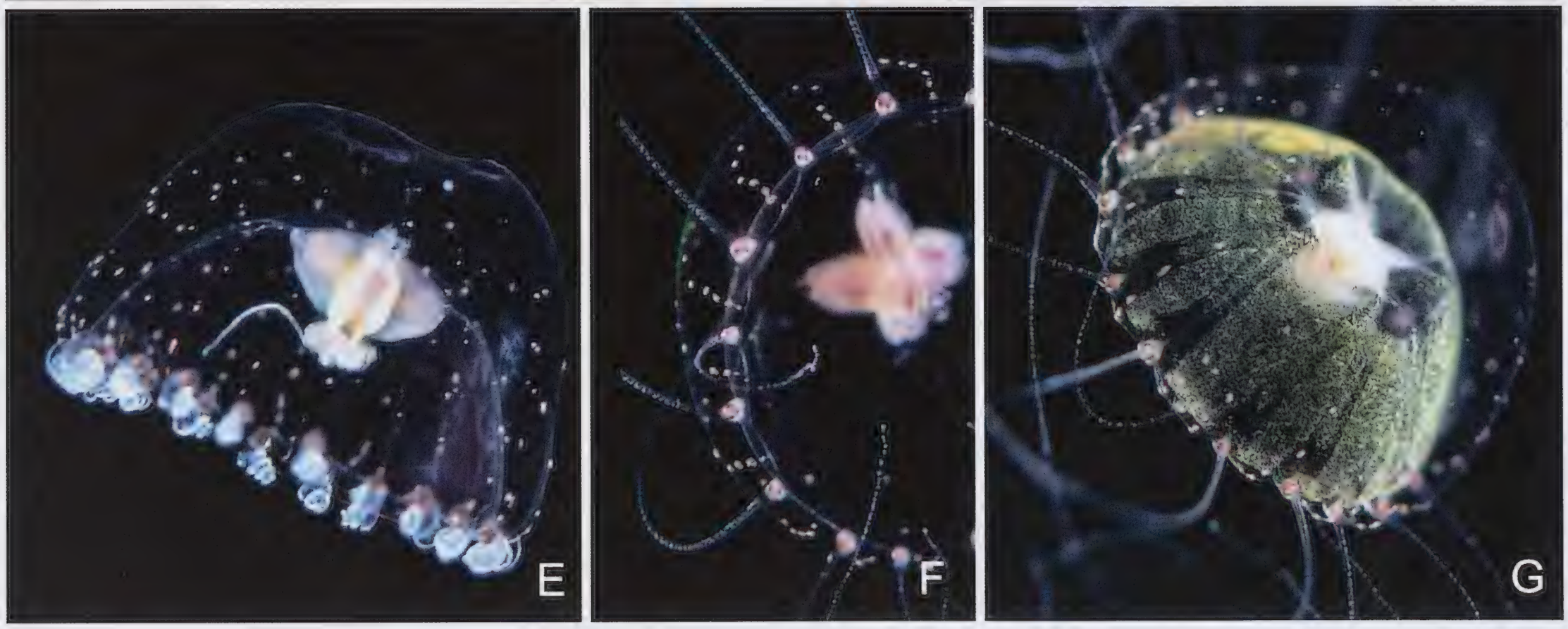


Fig. 14. *Proboscidactyla ornata*. Note that the usage of a flash brightens very much the exumbrellar nematocysts. (A-C) BFLA4357, bell size 5 mm, mature female, note that there are five radial canals leaving the manubrium. (D) BFLA4349, bell size 4 mm, subadult (?). (E) BFLA4356, bell size 4 mm, male. (F) Medusa photographed 13-MAR-2020, not collected, bell size 4 mm, note regular arrangement of exumbrellar nematocysts patches. (G) BFLA4354, bell size 4 mm, a layer of unidentified green particles is covering the subumbrella.

also had more nematocyst patches on the exumbrella, however, these are apparently lost rapidly in preserved material (likely also in net caught material). The maximum likelihood tree (Fig. 16) strongly suggests that our current concept of *P. ornata* comprises several mitochondrial lineages, *viz*. most likely species. This is also the reason why we separated the morphotype with medusa buds into a separate species (see below). Our medusae *P. ornata* were all rather fully grown, at least some with developed gonads. Because vegetative medusa budding might only occur in immature specimens, we cannot exclude that also *P. ornata* can have such a medusa budding. In this context, an observation noted by Mayer (1910) is interesting. He states that the budding variety of *P. ornata* is confined to the region south of South Carolina, while the non-budding form occurs from Florida up north to New England. Agassiz (1865, Buzzards Bay), Fewkes (1882a, Tortugas), and Calder (1970, Virginia) raised the medusa and did not report vegetative budding. This can be interpreted as two species with differing distributions being present. The northern limit of the budding form must be corrected to at least North Carolina as the type specimen of *P. gemmifera* (Fewkes, 1882) came from Beaufort Inlet.

Proboscidactyla gemmifera (Fewkes, 1882)
Fig. 15A-F

Willia gemmifera Fewkes, 1882b: 300, pl. 1 fig. 24.
Proboscidactyla gemmifera. – Browne, 1905: 727.
Dyscannota gemmifera. – Mayer, 1900: 47, pl. 8 fig. 17.
Proboscidactyla ornata var. *gemmifera.* – Mayer, 1910: 192, fig. 101a, pl. 21, figs 1-3.

Material examined: BFLA4285; 1 specimen; 06-DEC-2019; size 3 mm, 19 tentacles, with medusa buds; preserved in alcohol for DNA extraction; 16S sequence MW528699. – BFLA4321; 1 specimen; 24-JAN-2020; size 2.5 mm, 17 tentacles, with medusa buds; preserved in alcohol for DNA extraction; 16S sequence identical to MW528699. – BFLA4338; 1 specimen; 07-FEB-2020; size 3 mm, 18 tentacles, with medusa buds; preserved in alcohol for DNA extraction; 16S sequence identical to MW528699. – 24-JAN-2020; 1 specimen photographed, not collected; 3 mm, 14 tentacles, with medusa buds.

Observation: Medusae as described for *P. ornata* but somewhat smaller, 2.5-3 mm, though none of them appear sexually mature, tentacle numbers 14-19, more nematocyst patches on exumbrella, these often quite irregular and some not in linear arrays, no dark pigment in gastrodermis of tentacle bulbs. The most notable difference is the presence of four blastostyles (Fig. 15C) at each of the proximal-most branching points of the radial canals. Blastostyle resembling a polyp with one short capitate tentacle (visible in Fig. 15A, C) and bearing one to several medusa buds of different development stages.

16S Data: See Table 1 and Fig. 16.

Distribution: NE Atlantic from Cape Hatteras to Florida, likely more widely spread but identifications are unreliable (see *P. ornata*). Type locality: USA, North Carolina, Beaufort Inlet.

Remarks: Although the three samples used to obtain 16S sequence data were collected at different dates they all proved to be identical and clearly distinct from *P. ornata* (Fig. 16). This clade seems to be about equally distant from *P. ornata* as it is from the Pacific *P. flavicirrata* Brandt, 1835. This evident barcoding gap argues for it representing a distinct species.
The observed morphological differences to the sympatric *P. ornata* are listed above. It must be noted that *P. gemmifera* were found during the winter months, while the mature *P. ornata* were seen from March to June.
Proboscidactyla gemmifera was described based on a single medusa which was probably not fully developed as it had only eight tentacles (Brooks, 1880; Fewkes, 1882b). Mayer (1900, 1910) later supplemented more detailed descriptions of more advanced specimens from Florida. These descriptions do not agree with our specimens concerning the position of the blastostyles. Fewkes and Mayer found them at the junction of the radial canal to the manubrium, while in our samples they were located at the first bifurcation of the radial canals (Fig. 15A). This is not necessary a significant difference. Kramp (1957, 1962) found the blastostyles in every possible position along the radial canals, this in various populations from the Pacifc (identified as *P. ornata*). He regarded this variation as without any systematic importance.
Uchida & Sugiura (1975) examined the medusa bud development in a Japanese form of *P. ornata* and found that the position of the blastostyles is variable, depending on the developmental age (size) of the medusa. Smaller ones had them at the corners of the stomach, larger ones at the branching points. They also found that sexually mature medusae can continue budding medusae.
Although with some hesitation, we therefore referred our medusae to *Proboscidactyla gemmifera*.

Suborder Capitata
Family Sphaerocorynidae Prévot, 1959
Genus *Euphysilla* Kramp, 1955

Euphysilla Kramp, 1955b: 245; type species *Euphysilla pyramidata* Kramp, 1955 by monotypy.

Diagnosis: Medusa with pear- to egg-shaped umbrella in life; with apical chamber; manubrium with quadratic base; mouth circular; four equally developed tentacles with adaxial or abaxial nematocyst clasps and a

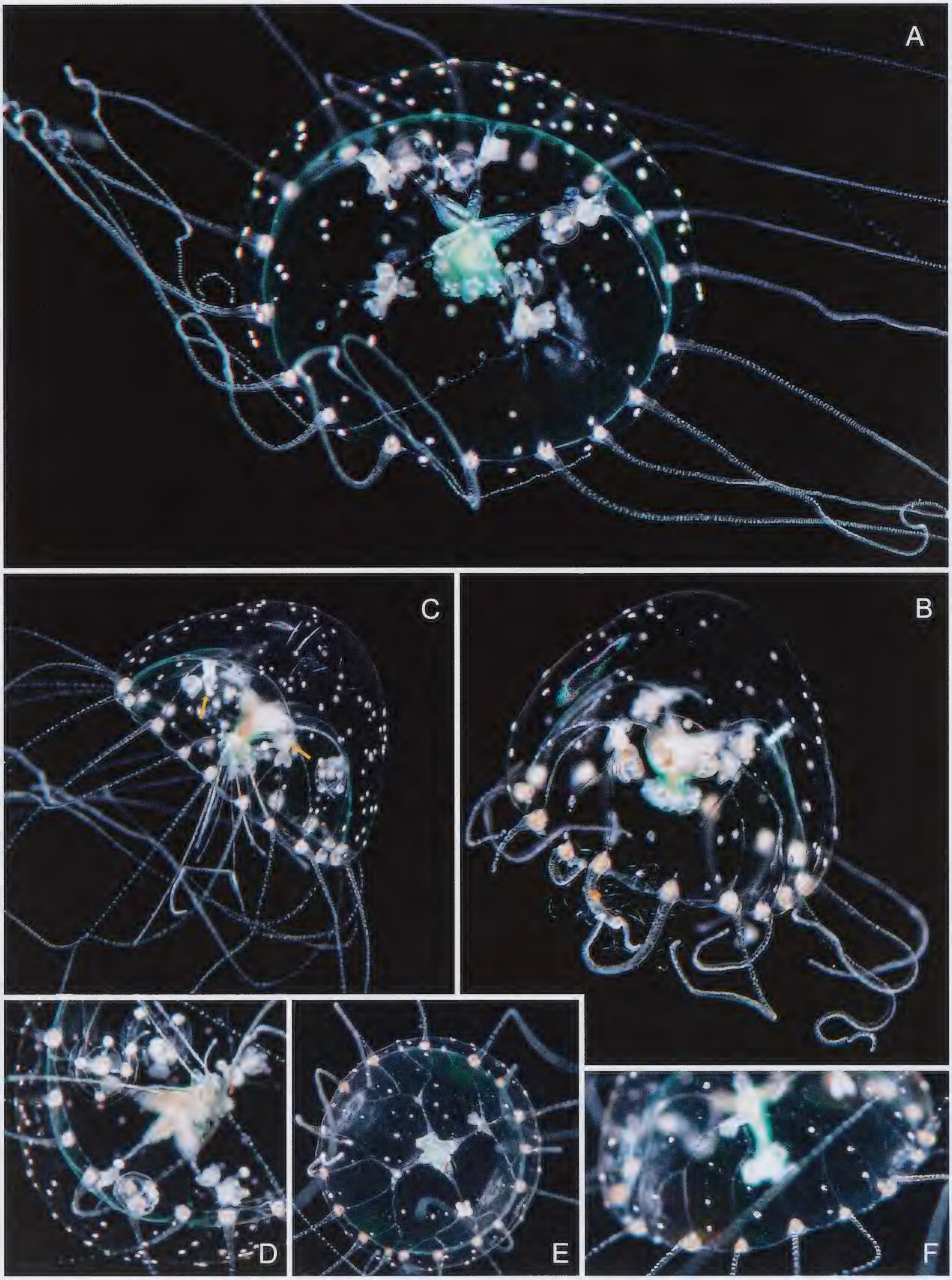


Fig. 15. *Proboscidactyla gemmifera.* Note that the usage of a flash brightens very much the exumbrellar nematocysts. (A) BFLA4338, diameter 3 mm. (B) Medusa photographed 24-JAN-2020, not collected, diameter 3 mm. (C) BFLA4285, lateral view, diameter 3 mm, arrows point to blastostyles (D) BFLA4285, oral view. (E) BFLA4321, aboral view. (F) BFLA4321, lateral view of bell margin, diameter 2.5 mm, note regular arrangement of exumbrellar nematocysts patches.

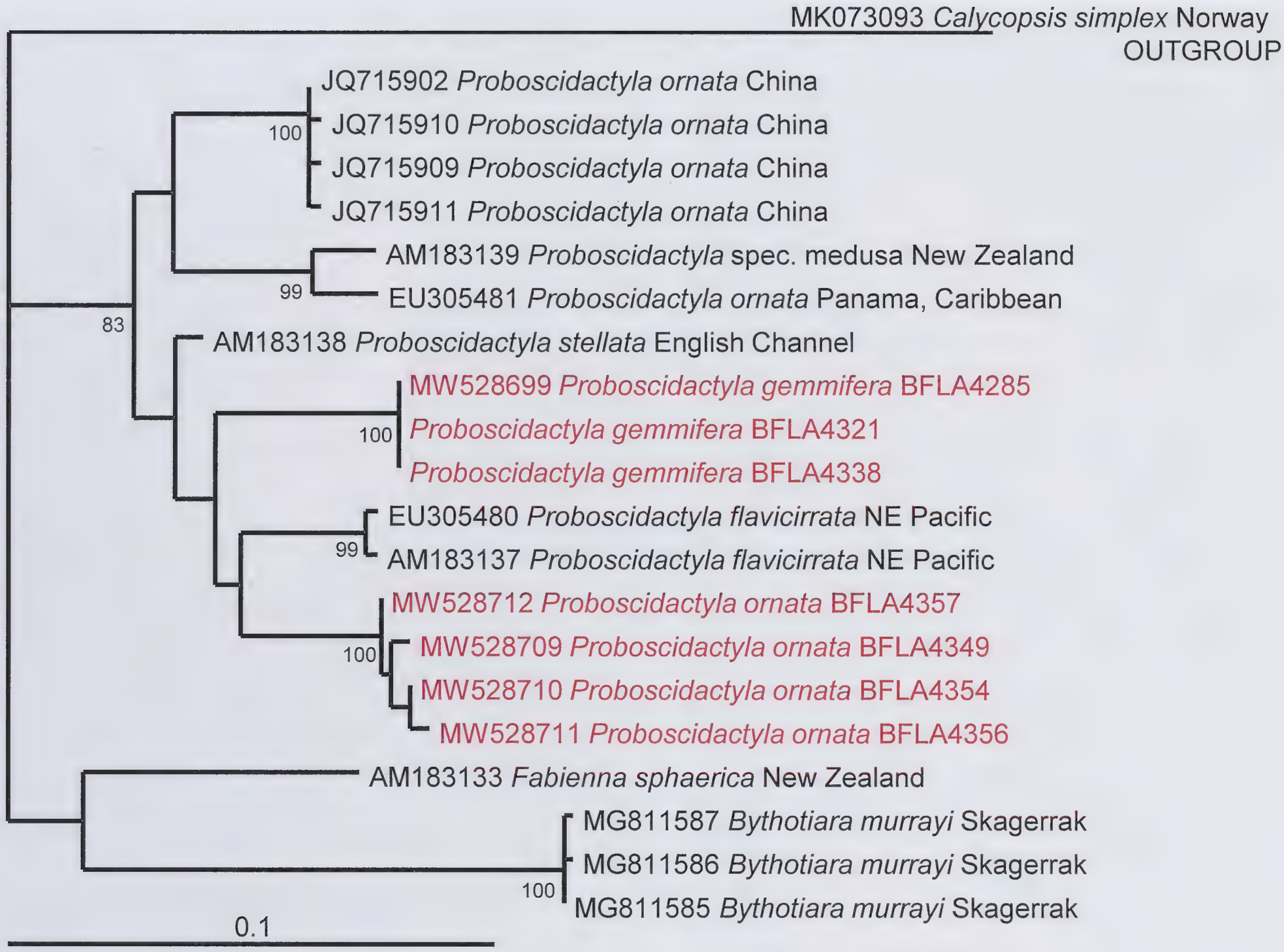


Fig. 16. 16S maximum likelihood phylogenetic tree of Proboscidactylidae and related taxa obtained with PhyML (GTR+G model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). All sequence labels start with the GenBank numbers permitting the retrieval of more information. Red labels are new sequences from this study. All samples are based on medusae.

terminal nematocyst knob; no gastric peduncle; mature gonads circular, surrounding manubrium; no ocelli. Usually with groups of medusa buds in middle part of manubrium.

Remarks: The diagnosis of *Euphysilla* of Bouillon *et al.* (2006) was here slightly modified by adding "with apical chamber" (see below). *Euphysilla pyramidata* appears indistinguishable from the genus *Sphaerocoryne* except for the medusa budding and the absence of ocelli. It is here associated with the Sphaerocorynidae following Petersen (1990, as suborder Sphaerocorynida incerta sedis).

Euphysilla pyramidata Kramp, 1955

Fig. 17A-I

Euphysilla pyramidata Kramp, 1955b: 245, pl. 1 fig. 1, pl. 2 fig. 3. – Kramp, 1959a: 90, fig. 42. – Kramp, 1961: 39. – Kramp, 1965: 4. – Kramp, 1968: 17, fig. 33. – Vannucci & Santhakumari, 1969: 40. – Schmidt, 1973: 16. – Hamond, 1974: 554, figs 4-6. – Segura-Puertas, 1984: pl. 2 fig. 2. – Petersen, 1990: 135, fig. 7B. – Xu & Huang, 2004: 560, fig. 9.

? not *Euphysilla pyramidata.* – Bouillon, 1978b: 259, figs 7 & 8.1-2.

Examined material: BFLA4396; 1 specimen; 17-MAY-2020; size 2.5 mm; preserved in ethanol for DNA extraction; 16S sequence MW528719. – BFLA4397; 1 specimen; 17-MAY-2020; size 2 mm; preserved in ethanol for DNA extraction; 16S sequence MW528720. – BFLA4402; 1 specimen; 26-MAY-2020; size 3 mm; preserved in formalin and deposited as UF-014043. – BFLA4468; 1 specimen; 17-JUN-2020; size 3 mm; preserved in formalin and deposited as UF-014073. – BFLA4478; 1 specimen; 18-JUN-2020; size 4 mm; preserved in ethanol for DNA extraction; 16S sequence identical MW528719.

Observations: Umbrella 2-4 mm in height, oviform, with apical thickening of very variable height, lateral walls thin, exumbrella with scattered nematocysts. Above manubrium an apical chamber, without apparent connection to gastric cavity, size variable depending on size of apical process (Fig. 17A-C). Manubrium an inverted cone, as long as bell cavity, base broad and cruciform in life (Fig. 17D), more square-shaped when preserved, upper part of manubrium cylindrical,

narrowing to tubular lower part of manubrium ending in small, circular mouth. All observed medusae were budding medusae, buds in groups on all four perradial sides of the manubrium in about the middle of the manubrium. Gonad-like opaque tissue layer covers manubrium above buds. Colour of manubrium intensively yellow-orange. Radial canals connected to manubrium by apparent short mesenteries (giving cruciform manubrium base), thin; circular canal more rectangular than circular. Four tentacles, contracted about half the length of the bell height, each with 8-12 crescent-shaped, clasping nematocyst pads, all in one row on adaxial side, terminal button ovoid, as wide as rest of tentacle. Four tentacle bulbs relatively small, orange-yellow, without well visible ocelli, but a faint reddish spots may be present on abaxial tentacle base (Fig. 17A).

Nematocyst (Fig. 17F-I, preserved tissue, sizes approximative): small stenoteles (7x10 µm), large stenoteles (12x13 µm), desmonemes (4x9 µm), spherical microbasic eurytele with barbed filament, shaft appears without barbs (7x10 µm).

16S Data: The three obtained 16S sequences represented two haplotypes, differing in only one base pair of 588. A blastn search in GenBank singled out a sequence (LT714182) with very high similarity (99.3%, Fig. 21). The sequence was obtained from a *Sphaerocoryne* polyp collected in the Maldives archipelago.

Distribution: Circumglobal in tropical seas. Western Africa (Kramp, 1955b); Gulf of Mexico (Segura-Puertas *et al*., 2003); Indian Ocean (Kramp, 1965; Vannucci & Santhakumari, 1969; Hamond, 1974); Red Sea (Schmidt, 1973); Bismarck Sea (Bouillon, 1978b); Taiwan Strait (Xu & Huang, 2004); tropical eastern Pacific Ocean from Peru to Mexico (Segura-Puertas, 1984). Type locality: Atlantic Ocean, Gulf of Guinea, off the coast of Bénin; WGS84 6.01667, 2.35000; depth 0-10 m.

Remarks: *Euphysilla pyramidata* has not been recorded frequently, this despite its apparent circumglobal distribution. Kramp's type specimen had no medusa buds, but he states that it had developed gonads. *Euphysilla pyramidata* with medusa buds were then reported in nearly all descriptions subsequent to Kramp (1955b, 1965) (see synonymy above). Hammond (1974) found both forms. Except for the medusa buds, our specimens matched Kramp (1955b) quite well, including the yellow manubrium colour, although in Kramp's formalin preserved material the remaining colour had become faint. The differences of our specimens and Kramp's description in the shape of the manubrium (quadratic versus cruciform manubrium base, wide mouth versus narrow) can easily be attributed to fixation artefacts, *viz*. the type specimen having been preserved with an inflated stomach. Moreover, the stomach base depicted by Kramp (1955b: pl. 2 fig. 3) is more cruciform than quadratic. Kramp (1955b) did not mention an apical chamber, but his figure 1 on plate 1 shows such a chamber, although only faintly.

Euphysilla pyramidata medusae reported from the Pacific Ocean by Bouillon (1978b) have some differences to our material. First, the apical thickening, hence likely also the apical chamber, is absent and the umbrella is more spherical, thus unlike the type specimen figured in Kramp (1955b). Second, Bouillon (1978b) also describes the colour of the manubrium as rose-orange and the one of the bulbs as having a hue of red. Whether these are species level or population level differences remains to be investigated by genetic examinations. Perhaps Bouillon's medusae are referrable to *Euphysilla tubularia* Huang, Xu & Lin, 2015, from which they appear not objectively separable. The tubular part of the manubrium in the mouth region in *Euphysilla tubularia* is certainly only a fixtion artefact. We observed the same in the present material.

It is thus probable that *E. pyramidata* as currently perceived is a complex of species. As in other genera, including information on the polyp stage might change its scope.

The 16S sequences gave a surprising match with a hydroid of the genus *Sphaerocoryne* from the Maldives (LT714182, Maggioni *et al*., 2017). The author of this sequence, Dr Davide Maggioni, kindly let us know that a publication describing this colony is currently in preparation.

Family Zancleidae Russell, 1953
Genus *Zanclea* Gegenbaur, 1857

Synonymy: See Schuchert (2010).

Diagnosis: Newly liberated medusae with two opposite tentacles, umbrella bell-shaped, four perradial exumbrellar nematocyst patches or tracts containing stenoteles; four radial canals; with two or four marginal tentacles when fully grown, tentacles with numerous abaxial extensile cnidophores containing macrobasic euryteles; mouth simple, circular; gonads inter-radial; no ocelli.

Hydroid stage colonial, with stolonal hydrorhiza, polyps sessile or with pedicels, usually unbranched, polyps monomorphic or polymorphic, when polymorphic polyps may be differentiated into gastrozooids, gonozooids, and dactylozooids; gastrozooids elongated, cylindrical or claviform, always with capitate tentacles, tentacles usually numerous and scattered over body, in some species reduced to a few tentacles; gonozooids and dactylozooids, when present, resembling reduced gastrozooids. Gonophores liberated as free medusae or rarely medusoids. Cnidome includes stenoteles and macrobasic euryteles, the latter type may be absent in the polyp stage.

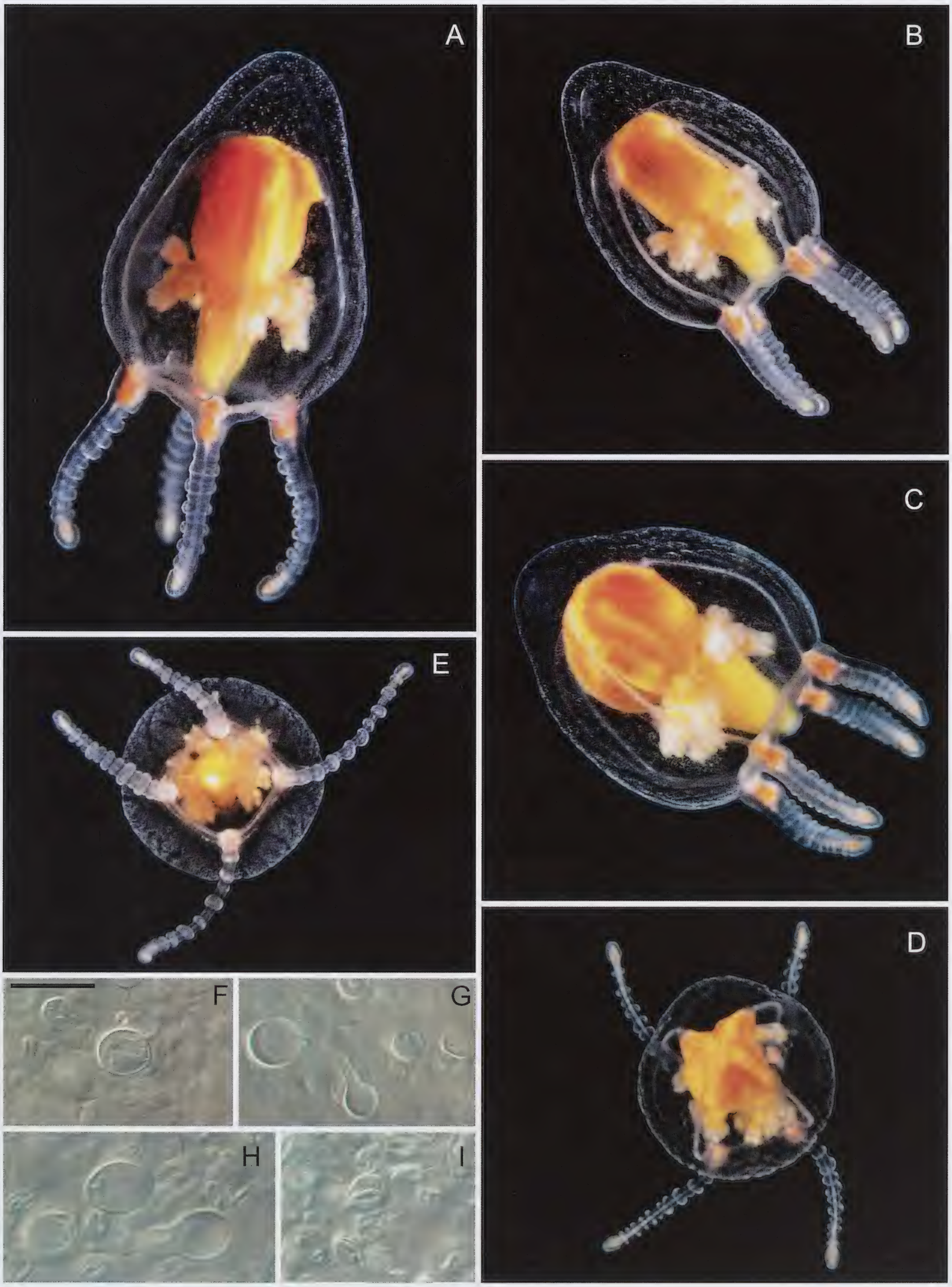


Fig. 17. *Euphysilla pyramidata*. (A-B) BFLA4396, bell height 2.5 mm. (C-D) BFLA4468, bell height 3 mm. D in aboral view, note cruciform manubrium base. (E) BFLA4397, oral view, bell height 2 mm. (F-I) Nematocysts of alcohol preserved tissue, scale equals 20 μm, valid for F to I. (F) Undischarged microbasic eurytele. (G) Discharged microbasic eurytele, stacked photo. (H) Intact and discharged large stenotele. (I) Desmonemes.

Remarks: For the identification of many *Zanclea* species it is usually necessary to know the hydroid stage (Boero *et al.*, 2000; Puce *et al.*, 2002; Maggioni *et al.*, 2018; Schuchert, 2010). Some Teisseriidae hydroids also produce *Zanclea*-like medusae, but they have ocelli.

Boero *et al.* (2000) critically reviewed all known *Zanclea*, *Zanclella*, and *Halocoryne* and described several new species. Subsequently, a bewildering number of new species were described, based either solely on the medusa or the polyp stage (e. g. Gershwin & Zeidler, 2003; Puce *et al.,* 2002; Galea, 2008; Puce *et al.*, 2008; Xu *et al.,* 2008; Pantos & Bythell, 2010; Hirose & Hirose, 2012; Varela, 2012; Montano *et al.*, 2015; Pica *et al.*, 2017). A molecular phylogeny was provided by Maggioni *et al.* (2018). It is now clear that the genus *Zanclea* is enormously diverse and the lumping of several nominal species into *Zanclea costata* as in Russell (1953) or Kramp (1959a, 1968) is not tenable anymore.

Zanclea mayeri n. spec.

Figs 18A-E, 19A-H

Zanclea costata. – Mayer, 1910: 87, pl. 8 fig. 6, perhaps also 2, 3, 7. [not *Z. costata* Gegenbaur, 1857]

Holotype: BFLA4061; photographed (Fig. 18A-E) and collected 10-APR-2019; 6 mm high, 3 mm wide; preserved in alcohol and used entirely for DNA extraction; frozen DNA solution deposited in MHNG under the catalogue number MHNG-INVE-0137375; 16S sequence MW528663.

Paratypes: BFLA4219; 1 specimen; 27-SEP-2019; height 5 mm; preserved in alcohol for DNA extraction; frozen DNA solution deposited as MHNG-INVE-0137377; 16S sequence MW528687. – BFLA4281; 1 specimen; 06-DEC-2019; height 7 mm; preserved in alcohol for DNA extraction; frozen DNA solution deposited as MHNG-INVE-0137378; 16S sequence MW528697. – BFLA4297; 1 specimen; 09-DEC-2019; height 6 mm, width 4 mm; preserved in alcohol for DNA extraction; frozen DNA solution deposited as MHNG-INVE-0137380; 16S sequence MW528703.

Type locality: USA, Florida, 5.5-12 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Etymology: The name honours Alfred Goldsborough Mayor [Mayer] who described this species in his outstanding work of 1910 (for a biography see Stephens & Calder, 2006).

Description: Mature medusa 4 to 7 mm high and 3-4 mm wide, bell bullet-shaped, apex rounded, lateral wall straight. Mesoglea relatively thick, thicker at apex. Exumbrella with four thick, white perradial nematocyst bands, protruding from surface, reaching from circular canal to apex, two opposite bands often recurved at apex (Fig. 18A-C). Subumbrella with interradial pockets projecting into apical mesoglea (Fig. 18A-B). Manubrium large, composed of a larger upper part and a thinner, short, cylindrical mouth region. Upper part of manubrium with cruciform cross-section (Fig. 19B), gonads cover surface entirely as a thin layer, but separated perradially. Radial canals smooth. Only two tentacles, opposite, other two perradial positions without bulbs. Tentacles at base thick, without bulb formation, evenly tapering to very fine end, very contractile or extensible to more than 35 mm (Fig. 18E). Tentacles with abaxial row of cnidophores, these relatively large, spherical, with long, contractile stalk (Figs 18E, 19D). No ocelli present. Colours: manubrium orange (females) or faintly orange (males), tentacles faint pink-orange. Nematocysts: macrobasic euryteles and stenoteles (Fig. 19F-H).

One medusa (Fig. 19E) with a hydroid colony growing on upper part of manubrium, polyp with one whorl of few capitate tentacles, stolon-like processes in the manubrium tissue. It is not evident if this hydroid is derived from medusa or if it is a parasitic hydroid.

16S data: The four available samples gave four different 16S haplotypes with divergences of 0.8-1.2%. A blastn search in GenBank with the obtained sequences yielded numerous *Zanclea* sequences, but all with less than 92% identity. A maximum likelihood tree using part of the 16S sequence data of Maggioni *et al.* (2018) did not associate the sample with any other (Fig. 21).

Remarks: Mayer (1910) described and figured a single *Zanclea* medusa from Florida which he attributed to *Zanclea costata* Gegenbaur, 1857. His figure (pl. 8 fig. 6) obviously depicts the same medusa as shown here in Figs 18-19. Also, the size was the same (6 mm) and the umbrella shape matches. The scope of *Z. costata* has changed since then, although the identity of Gegenbaur's medusa from the Mediterranean is still not entirely resolved (Brinckmann-Voss, 1970; Boero *et al.*, 2000; Cerrano *et al.*, 1997; Schuchert, 2010; Maggioni *et al.*, 2018). Gegenbaur's medusae were relatively big (2-5 mm), had four tentacles, and the nematocyst bands reached up to the apex. However, medusae that exactly matched Gegenbaur's medusa have never been found again and the current scope of *Z. costata* goes back to Brinckmann-Voss (1970). The Mediterranean *Z. costata* has four marginal bulbs even in younger stages and with optimal growth it will develop four tentacles (Gegenbaur, 1857; Brinckmann-Voss, 1970; Schuchert, 2010). *Zanclea mayeri* is even larger than *Z. costata* but has only two tentacles and two bulbs. The divergence of the 16S from *Z. costata* (GenBank entry FN687559) is 9% and 8.5% from an unidentified Mediterranean *Zanclea* with four tentacles (GenBank entry KP776810). *Zanclea mayeri* is distinct and does not match any of the

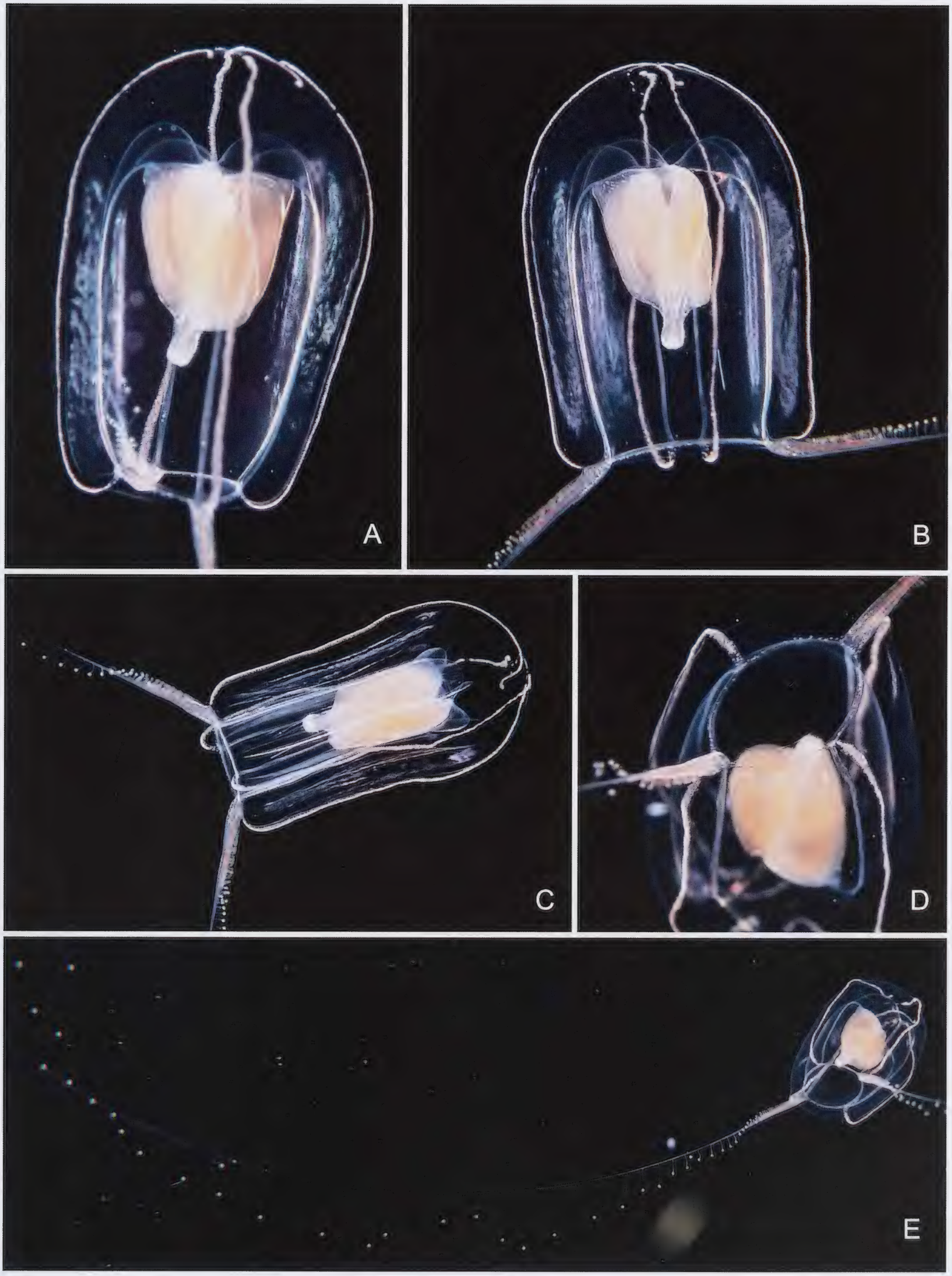


Fig. 18. *Zanclea mayeri* n. spec., living holotype specimen, BFLA4061, bell height 6 mm (A-C) Lateral views. (D) View on umbrella opening. (E) Animal with one tentacle fully extended.

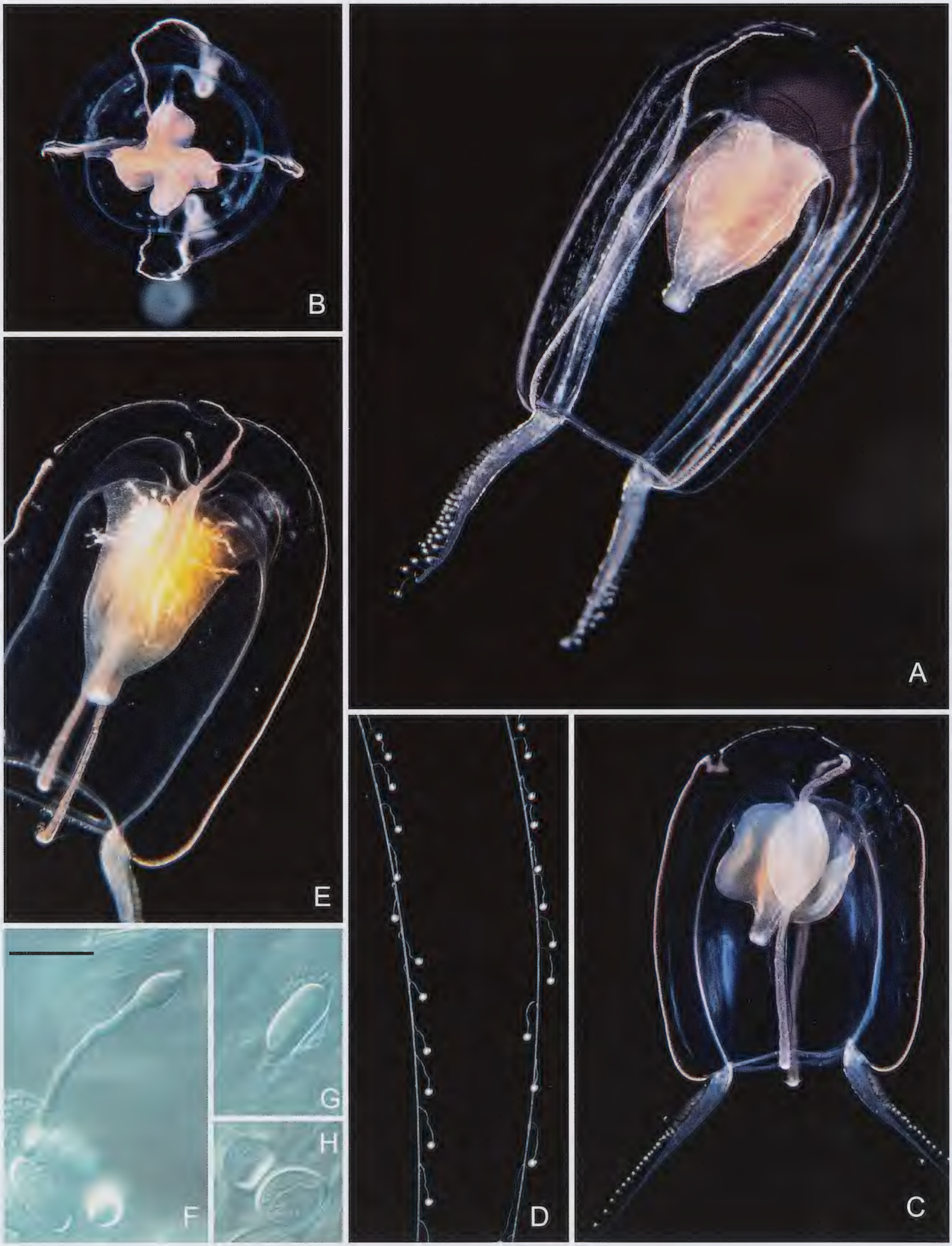


Fig. 19. *Zanclea mayeri* n. spec. (A) BFLA4281, female with oocytes in gonad, height 7 mm. (B) BFLA4281, view from aboral side. (C) BFLA4297, height 6 mm. (D) BFLA4219, part of extended tentacles. (E) BFLA4219, note the capitate polyps growing in the upper part of the manubrium wall, height 5 (F-G) BFLA4219, alcohol preserved nematocysts; scale bar 20 μm. (F) Discharged macrobasic eurytele. (G) Intact macrobasic eurytele, stacked photo. (H) Stenotele.

known nominal *Zanclea* species. We therefore introduce it as a new nominal species.
The holotype specimen of *Zanclea mayeri* n. spec. was used entirely to extract its DNA. The deposited type material is thus not a preserved specimen but only part of it as an extract of its genomic DNA in a buffered solution. A DNA solution serving as type specimen has so far not been used for any hydrozoan, but it is in accordance with the International Code of Zoological nomenclature as it can be regarded as a part of the type specimen (Article 72.5.1). Moreover, photos of the living holotype specimens are given in Fig. 18A-E and applying article 72.5.6 of the ICZN the depicted specimen becomes the type specimen.

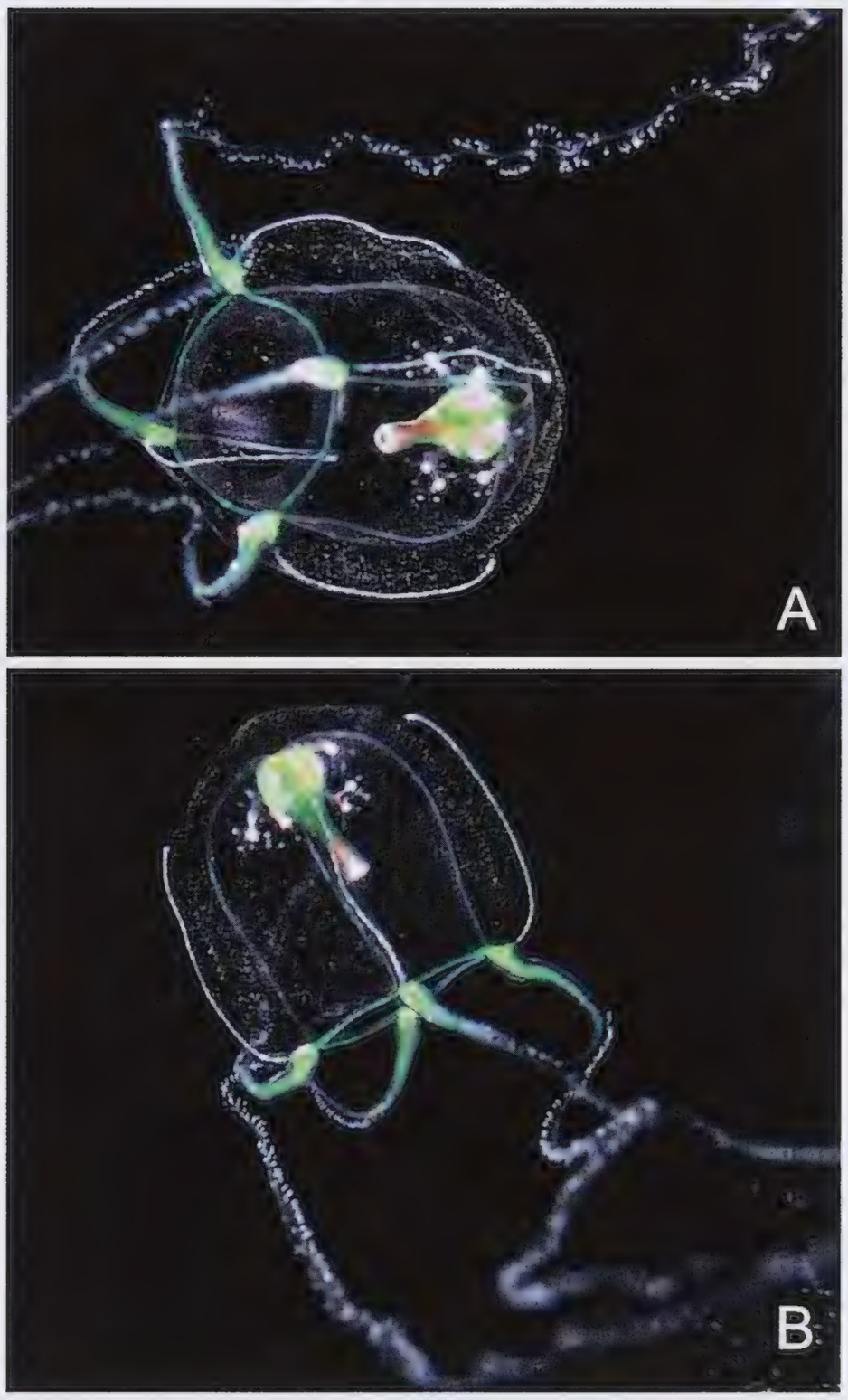


Fig. 20. *Zanclea* spec. (A-B) BFLA4278, bell height 2 mm.

Zanclea spec.
Fig. 20A-B

Examined material: BFLA4278; 1 specimen; 06-DEC-2019; height 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528696.

Observations: *Zanclea* medusa, height 2 mm, bell as wide as high, apical part a flat cone. Four exumbrellar nematocyst bands reaching from tentacle bulbs to level of manubrium base (ca. 4/5 of bell height). Manubrium relatively small, bottle-shaped, in upper part with several polyps, these sessile, partly embedded, cylindrical body, with up to three whorls of capitate tentacles. Gonads apparently not yet developed. Four equally well-developed marginal tentacles with stalked cnidophores, no distinct bulb formation, tentacles evenly tapering from origin to distal. No ocelli present. Upper, broader part of manubriumas well as tentacles intensively green.

16S Data: A maximum likelihood tree using part of the 16S sequence data of Maggioni *et al.* (2018) did not associate the sample with any other (Fig. 21). The sequence is rather distinct from those of *Z. mayeri* n. spec. as it shares only 91% identical base pairs.

Remarks: Only one immature animal of this striking *Zanclea* species was observed. The green colour, the four tentacles, and the hydranths on the stomach make it rather unique. Although it is likely an undescribed species, we nevertheless renounced on naming it as we think that we do not have enough photos showing more details for a complete description. It is also immature and the polyps could be a parasite or some teratological development and not a normal feature of the species.
The animal resembles *Zanclea medusopolypata* Boero, Bouillon & Gravili, 2000 from Papua New Guinea, but the latter has only two tentacles. Although tentacle numbers can be variable in *Zanclea* species (Brinckmann-Voss, 1970; Altuna, 2016) it should not be referred to *Z. medusopolypata* for biogeographic reasons and because its polyp stage remains unknown.

Family Zancleopsidae Bouillon, 1978
Genus *Zancleopsis* Hartlaub, 1907

Diagnosis: Medusa with or without apical projection; four tentacles, either two long, opposed, capitate tentacles with capitate side branches and two opposed, shorter, simple capitate tentacles, or with four simple capitate tentacles; marginal tentacular bulbs clasping umbrella margin, bulbs with large hemispherical adaxial bulges covered with nematocysts, with abaxial ocelli; manubrium flask-shaped; mouth more or less cruciform, with or without simple lips; gonads interradial to adradial, smooth with interradial cleft or more adradial pads or vertical folds. Polyp stage unknown.

Remarks: The affinities of this genus were obscure for a long time. Hartlaub (1907) placed it in the Zancleidae, Mayer (1910) and Kramp (1961) in the Cladonematidae, Kramp (1965, 1968) in the Pandeidae. It was only when Bouillon (1978b) examined the cnidome it became clear that the presence of stenoteles excluded the Pandeidae, while the desmonemes excluded the Zancleidae. Because also the Cladonematidae differ considerably, Bouillon (1978b) proposed the new family Zancleopsidae to accommodate it. The family currently

Fig. 21. 16S maximum likelihood phylogenetic tree of Zancleidae and related taxa obtained with PhyML (GTR+G model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). All sequence labels start with the GenBank numbers permitting the retrieval of more information. Red labels are new sequences from this study.

also includes the genus *Dicnida* Bouillon, 1978b (Bouillon *et al.*, 2006), but it is unclear if it belongs to the suborders Capitata or Aplanulata. Our results presented below show that the family belongs to the Capitata.

The species delimitations within the genus *Zancleopsis* are not well worked out, despite the comparisons or keys given in Bouillon (1978b, 1985) or Wang *et al.* (2016). The differences are mostly either due to mutilated- or to juvenile specimens having not yet developed diagnostic traits (Bouillon, 1978b).

Zancleopsis dichotoma (Mayer, 1900)

Figs 22A-F, 23A-F

Gemmaria dichotoma Mayer, 1900: 35, pl. 17 fig. 40.

Zancleopsis dichotoma. – Hartlaub, 1907: 115, fig. 105. – Mayer, 1910: 91, pl. 8 fig. 1. – Bigelow, 1938: 102, figs 1-2. – Kramp, 1959a: 95, fig. 53. – Kramp, 1961: 56. – Kramp, 1965: 25, correction of Kramp, 1959a. – Kramp, 1968: 39. – Bouillon, 1978b: 290. – Bouillon, 1985: Table 1.

Cnidotiara gotoi. – Kramp, 1959a: 12, pl. 1 figs 7-8. [misidentification, not *Zancleopsis gotoi* (Uchida, 1927)]

? *Zancleopsis dichotoma.* – Xu *et al.*, 2014: 363, fig. 228, juvenile specimen.

Examined material

Small form: BFLA4170; 1 specimen; 09-AUG-2019; size 3 mm; preserved in alcohol for DNA extraction; 16S sequence MW528683. – BFLA4171; 1 specimen; 09-AUG-2019; size 3 mm; preserved in alcohol for DNA extraction; 16S sequence MW528684. – BFLA4248; 1 specimen; 23-NOV-2019; size 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528692. – 13-AUG-2019, 3 mm, 1 specimen photographed, not collected. – 16-OCT-2019, no size estimate, 1 specimen photographed, not collected.

Large form: BFLA4408; 1 specimen; 26-MAY-2020; height 15 mm, 5 mm wide, male; preserved in alcohol for DNA extraction; 16S sequence MW528723. – BFLA4436; 1 specimen; 07-JUN-2020; height 12 mm, female; preserved in formalin and deposited as UF-014054. – BFLA4467; 1 specimen; 17-JUN-2020; height 15 mm, 5 mm wide, female; preserved in formalin and deposited as UF-014072, part of broken tentacle

preserved in alcohol for DNA extraction; 16S sequence MW528732. – 11-APR-2019; 1 specimen photographed; size 10-15 mm, with male gonads; not collected.

Observations

Small form (Fig. 22): Total bell height up to 3 mm, 1/4 to 1/3 of the height taken by pointed apical process; umbrella bell-shaped to conical, relatively thick walls, with shallow interradial subumbrellar pockets, tip of apical process green (Fig. 22A, E). Manubrium height about half the subumbrellar height when gonads start to develop, pear-shaped, short tubular oral part, mouth rim with four perradial white regions, upper part of manubrium (stomach) ochre coloured, with about 10 longitudinal, shallow gonad folds, folds mostly adradial, irregular. Radial canals not forming mesenteries, smooth. Tentacle bulbs all equally developed, almost spherical, placed adaxial of origin of tentacles, white or faintly yellow. Two long, opposite tentacles, much extendable/contractible, with up to 25 short, abaxial, side branches ending in nematocyst knobs, size of knobs gradually increasing towards distal (Fig. 22F). The other tentacle pair very short, ending in spherical nematocyst knob. In youngest animals observed these short tentacles either missing or just beginning to develop (Fig. 22E). All tentacle bases with a red ocellus on abaxial side.

Nematocysts (alcohol preserved tissue, BFLA4171): larger stenoteles [(24-26)x(22-23) µm], smaller stenoteles [(18+21)x(14-17) µm], desmonemes [8.5x5 µm], and macrobasic euryteles [(15-16)x(6-7) µm].

Large form (Fig. 23): Much larger than small form, height 8 to 15 mm and 5 mm diameter, apical process larger reaching 1/2 of total height, tip of apical process whitish, gonads always present, more and larger vertical gonad folds, approximately up to 15, 2-3 folds adradial, brownish, oocytes yellow (Fig. 23A), tentacle bulbs with intense yellow colour, shorter tentacle pair longer than in small form, sometimes terminal knob missing (Fig. 23B).

16S Data: The haplotypes of the small form differed in 0.5-0.8% of the base pairs, in the large form 0.3%. The maximal divergence observed between the two forms was 6.2% base pair difference.

The maximum likelihood analysis (Fig. 21) identified *Astrocoryne cabela* Maggioni *et al.*, 2017 polyps from the Red Sea and the Maldives Islands as relatively closely related, if not conspecific.

Distribution: Florida, Bermuda Islands, mid North Atlantic, Brazil (Kramp, 1959a; Navas-Pereira, 1980). Type locality: USA, Florida, Dry Tortugas archipelago. The record for the China Sea (Xu *et al.*, 2014) is based on a juvenile, indeterminable animal.

Remarks: This is a rare species of which only a few specimens have been reported. Our samples separated into two size categories which also had slight morphological differences, but explainable by different developmental stages being present. The smaller (bell size up to 3 mm) corresponded more to Mayer's (1910) description, while the larger ones corresponds to Bigelow's (1938) specimen. The only difference to Bigelow's material was the length of the tentacles and the presence of terminal knobs in the shorter pair of tentacles. However, this is easily explained by damage during the collecting process of Bigelow's material. Also Kramp (1965: 25) observed that the distal parts of the tentacles are often lost in net material. In one of our specimens, one knob was also missing (Fig. 23B). Mayer (1900) described *Gemmaria dichotoma* based on several, but apparently all immature medusa of 3 mm bell height. He characterised them as having only a single pair of branched tentacles. This is certainly attributable to the rather young stages he had. Also in some of our younger stages the short tentacles were either just developing or absent (Fig. 22E).

Were it not for the 16S results, we would have attributed without hesitation the two forms to two different developmental stages of the same species. The 16S barcode sequences separated the large and small forms into two distinct lineages (Fig. 22) which differed maximally in 6.2% of their aligned bases. We have no reference values of what constitutes intraspecific variation for this family, but the value is quite high compared to other species (comp. Table 1).

Due to the absence of any other diagnostic feature, we preferred for the moment to regard these two forms as belonging to the same species and representing younger and older stages. Many hydromedusae are known to continue their growth even when their gonads get mature. Note also that both forms were found at different times of the year (August to October versus April to June). If the two forms belong to the same species, then the differences in the 16S sequences deserves nevertheless some thoughts, beyond the possibility that they are simply stochastic variations observed in the small number of specimens. It can be argued that the larger forms are certainly also older and have thus spent more time in the current of the Gulfstream. This would then imply that the two forms come from quite different localities, the different 16S haplotypes might therefore come from separate populations.

Kramp (1968: 39) suspected that *Z. dichotoma* and *Z. tentaculata* are conspecific [for descriptions of *Z. tentaculata* see Kramp (1965, 1968) and Bouillon (1978b)]. Bouillon (1978b; 1985) kept them distinct, but he also had some doubts about the suitability of the distinguishing traits. Some of them are linked to the developmental stage (size and shape of bell, position and shape of the gonads, length and form of tentacles), others are clearly due to damages and losses during the collecting process (tentacle lengths and terminal knobs).

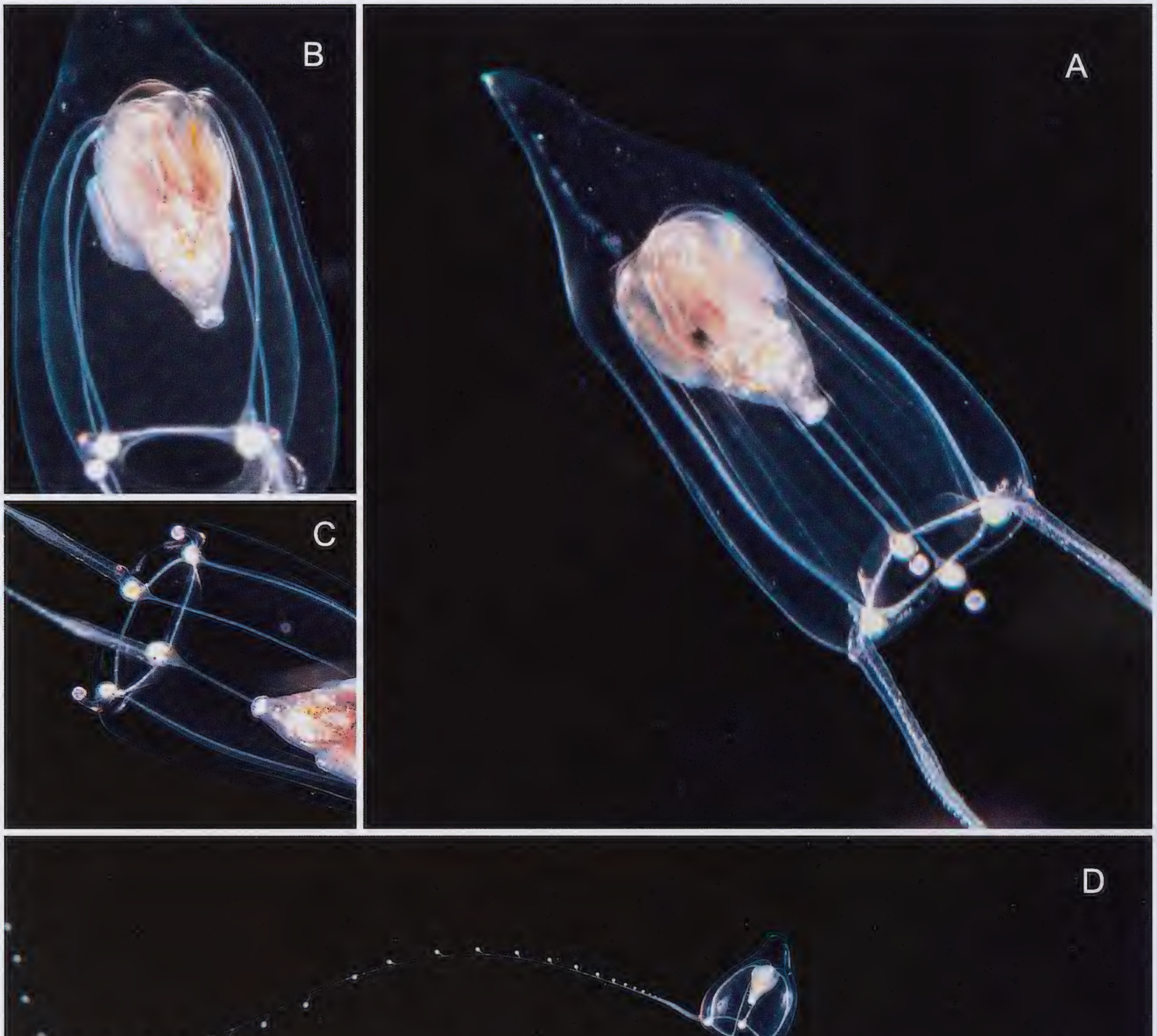


Fig. 22. *Zancleopsis dichotoma,* small form. (A-C) BFLA4171, bell height 3 mm, stomach filled with prey items, note well developed short tentacles. (D) BFLA4170, bell height 3 mm, gonads just begin to develop. (E-F) BFLA4248, bell height 2 mm, immature, note that one of the short tentacles (upper one) is only just developing, while the opposite bulb appears to be devoid of a tentacle.

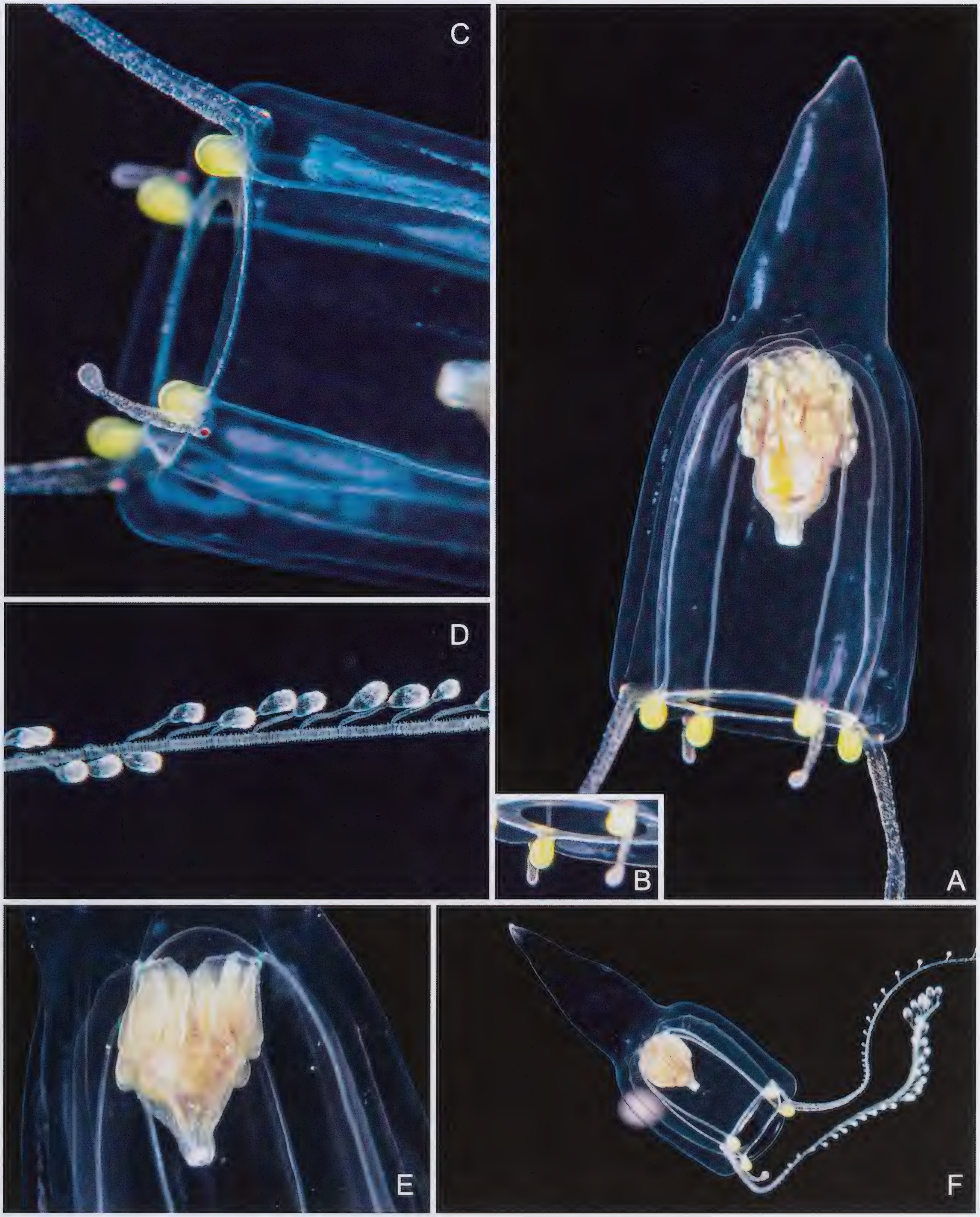


Fig. 23. *Zancleopsis dichotoma,* large form, sizes refer to the total bell height, including the apical process. (A-C) BFLA4467, size 12 mm, female, note in B that one of the short tentacles lacks a terminal knob. (D) BFLA4436, size 10 mm, part of long tentacles with capitate side branches. (E) BFLA4408, size 15 mm, close up of manubrium with male gonads. (F) Animal observed 11-APR-2019, size approximately 10-15 mm.

Suborder Aplanulata
Family Corymorphidae Allman, 1872
Genus *Corymorpha* M. Sars, 1835

Synonymy: See Schuchert (2010).

Diagnosis: Medusa bell apex dome-shaped or pointed. Four marginal bulbs present, without long exumbrellar spurs. With a single tentacle or three short tentacles and one long tentacle that differs not merely in size, but also in structure. Manubrium thin-walled, sausage-shaped with flared mouth rim, reaching to umbrella margin. Cnidome comprises stenoteles, desmonemes, and haplonemes.

Hydroids solitary with more or less vasiform hydranth and long caulus. Hydranth with one or several closely set oral whorls of 16 or more moniliform or filiform tentacles and one aboral whorl of 16 or more long, non-contractile filiform tentacles. Hydrocaulus stout, covered by thin perisarc, filled with parenchymatic gastrodermis, with long peripheral canals; aboral end of caulus with papillae turning more aborally into rooting filaments, rooting filaments composed of epidermis and solid gastrodermis, sometimes tips with non-ciliated statocysts. With or without asexual reproduction through constriction of tissue from aboral end of hydrocaulus. Gonophores develop on blastostyles arranged in a whorl over aboral tentacles. Gonophores remain either fixed as sporosacs or are released as free medusae.

Remarks: *Corymorpha* species usually have a rather simple medusa and a more complex hydroid stage offering more discriminating details. *Corymorpha* species that are solely based on the medusa stage are thus potentially species complexes which could be split into several species once their polyp stages become known. This is particularly pertinent for species with suspiciously wide distributions like *C. forbesii*.

Corymorpha forbesii (Mayer, 1894)
Fig. 24A-B

Hybocodon forbesii Mayer, 1894: 236, pl. 1 fig. 1. – Mayer, 1910: 42, pl. 1 fig. 8, pl. 2 fig. 3. – Vanhöffen, 1913a: 414. – Uchida, 1927a: 193, fig. 30.
Hybocodon forbesi. – Kramp, 1959a: 87, fig. 36. – Kramp, 1961: 42. – Kramp, 1968: 13, fig. 22. [incorrect spelling]
Hybocodon forbessi. – Nair, 1951: 50, pl. 1 fig. 1. [incorrect spelling]
Vannuccia forbesii. – Brinckmann-Voss, 1967: 1, figs 1-6. – Brinckmann-Voss, 1970: 14, figs 9-11, pl. 1 figs 1-2. – Schmidt, 1973: 17. – Bouillon, 1978b: 268. – Bouillon *et al.*, 2004: 93, fig. 49K-L.
Vannuccia forbesii f. *kanti* Bouillon, 1978a: 136.
Corymorpha forbesii. – Schuchert, 1996: 103, fig. 60a-c. – Schuchert, 2010: 386, fig. 15, synonymy, redescription.

Examined material: BFLA4045; 1 specimen; 01-APR-2019; preserved in ethanol for DNA extraction; 16S sequence MW528642. – 24-JUN-2019; 1 specimen photographed, with male gonads, not collected.

Observations: Umbrella bell-shaped, height size 2 mm, higher than wide, no apical process or a slight apical thickening, no exumbrellar nematocysts. Manubrium spindle-shaped, length about 2/3 of subumbrellar height, simple mouth, gonads encircle manubrium without interruption. Four large marginal bulbs, all of similar size or bulb opposite tentacle larger than the two other atentacular bulbs, bulb surface covered with

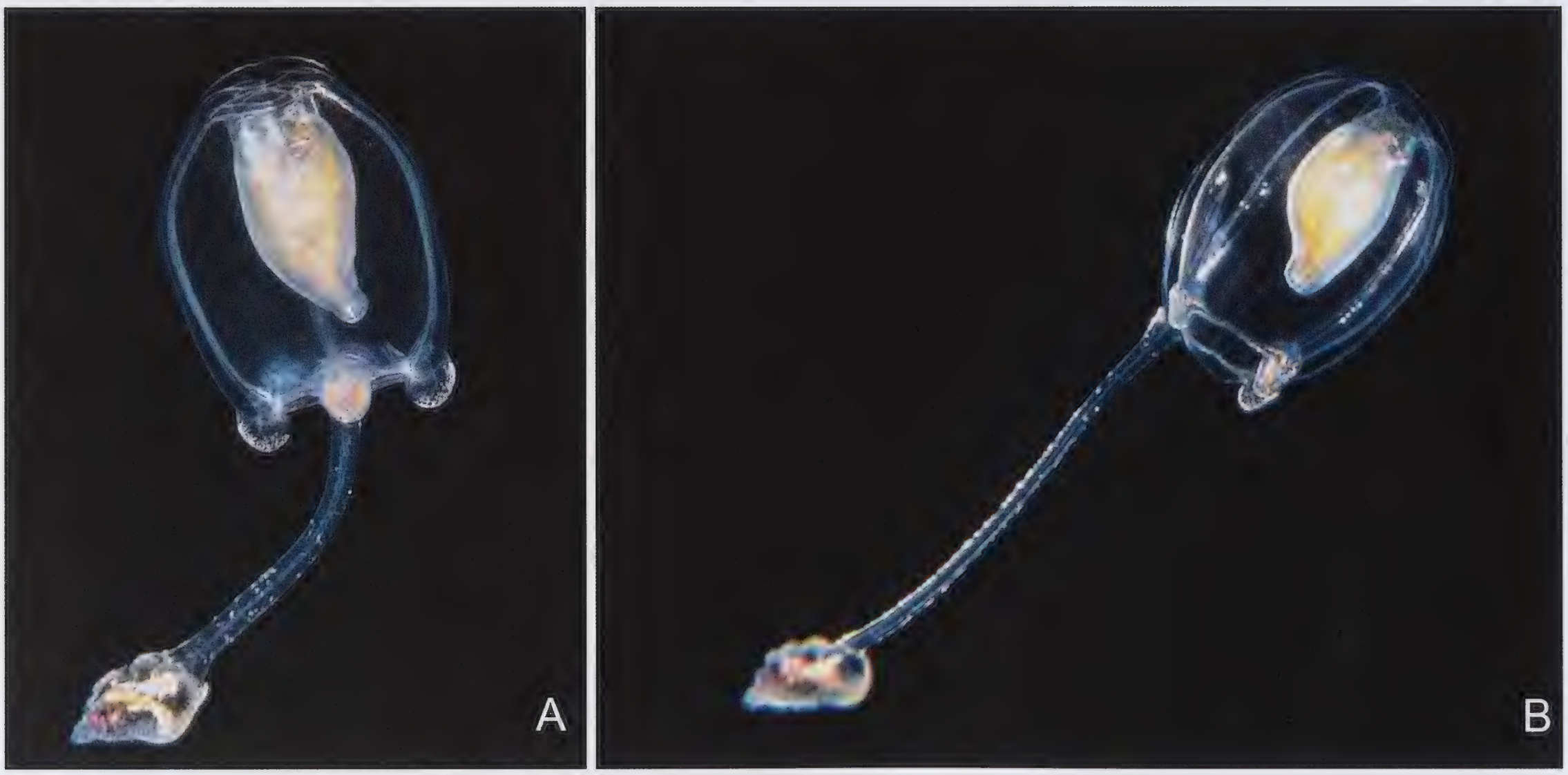


Fig. 24. *Corymorpha forbesii*, bell size ca. 2 mm (A) BFLA4045. (B) Specimen photographed in 24-JUN-2019.

nematocysts. Only one single tentacle, rather stiff, length 1.5 the bell height, 2/3 of length isodiametric and with only few nematocysts, distal third a club-shaped terminal swelling with numerous nematocysts.

16S Data: A blastn search in GenBank using the sole 16S indicated *Corymorpha glacialis* as best match, although with only 84% identity. This species was followed by other *Corymorpha* and Aplanulata species with similar low identify scores.

Distribution: Florida, Bahamas, Brazil, Mediterranean, Red Sea, Seychelles, India, Vietnam, Papua New Guinea, southern Japan, and New Zealand (Schuchert, 2010). Type locality: Bahamas; Nassau Harbour.

Corymorpha gracilis (Brooks, 1883)

Fig. 25A-B

Steenstrupia gracilis Brooks, 1883: 144.
Steenstrupia rubra. – Mayer, 1910: 31, pl. 1 fig. 7. [not *Steenstrupia rubra* Forbes, 1848 = *Corymorpha nutans* M. Sars, 1835]
Euphysora gracilis. – Kramp, 1959a: 89, fig. 40a. – Kramp, 1961: 40. – Goy, 1979: 269, fig. 2.
Corymorpha gracilis. – Nagata *et al*., 2014: 299, fig. 9.
not *Euphysora gracilis* – Pagès *et al.,* 1992: 20, fig. 18.

Examined material: BFLA4368; 1 specimen; size 4 mm; preserved in ethanol for DNA extraction; 16S sequence MW528715. – BFLA4401; 1 specimen; size 6 mm; preserved in ethanol for DNA extraction; 16S sequence identical to MW528715.

Observations: Umbrella bell-shaped, height 4 to 6 mm, about two times higher than wide, with very large, pointed apical process, often of the same size as the umbrella. No gastric peduncle. Manubrium tubular with some tapering towards mouth, length about 1/2 to 4/5 of the subumbrellar height, with long, conspicuous apical canal entering apical process (Fig. 25A-B), distal end often somewhat thickened and yellow in colour. Gonads wrapping manubrium entirely without perradial interruptions. Marginal tentacles of distinct types, one long, extensible tentacle with up to 7 large, oblong nematocyst clusters encircling tentacle entirely, some smaller annular nematocyst, clusters can be present, terminal cluster oblong and slightly thicker than annular ones. The annular clusters may be absent and only a few small clasping clusters can be present (likely in regeneration after tentacles loss). Other tentacles reduced to mere cones, the one opposite the longer tentacle about twice as long as the other two. Radial canals fine, but well visible due to white-yellowish pigmentation. Gastrodermis of tentacles with some red hues.

16S Data: A blastn search in GenBank using the sole 16S indicated *Corymorpha nutans* as best match, although with only 89% identity. This species was followed by other *Corymorpha* and Aplanulata species with similar low identity scores.

Distribution: Atlantic cost of the USA from New England to Florida (Brooks, 1883; Kramp 1959); Brazil (Kramp, 1959; Nagata *et al.,* 2014); South Atlantic (Goy, 1979). Doubtful records from the Benguela current (Pagès *et al*., 1992). Type locality: USA, North Carolina, Newport River.

Remarks: The specimen depicted by Pagès *et al.* (1992) and identified as *Euphysora gracilis* (syn. *Corymorpha gracilis*) lacked the typical large apical projection with the gastrodermal process in it. It is therefore not unambiguously attributable to *Corymorpha gracilis.*

Fig. 25. *Corymorpha gracilis.* (A) BFLA4368, total bell size 4 mm. (B) BFLA4401, size 6 mm.

Corymorpha floridana n. spec.

Fig. 26A-E

Holotype: BFLU4371; 1 formalin preserved male medusa deposited as FU-014026; collected 16-MAR-2020; bell height 3 mm.

Other examined material: BFLA4362; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence MW528714. – BFLA4363; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence identical to MW528714. – BFLA4364; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence identical to MW528714. – BFLA4365; 1 specimen; 13-MAR-2020; preserved in ethanol for DNA extraction; 2 mm bell; 16S sequence identical to MW528714. – BFLA4437; 1 specimen; 07-JUN-2020; preserved formalin and

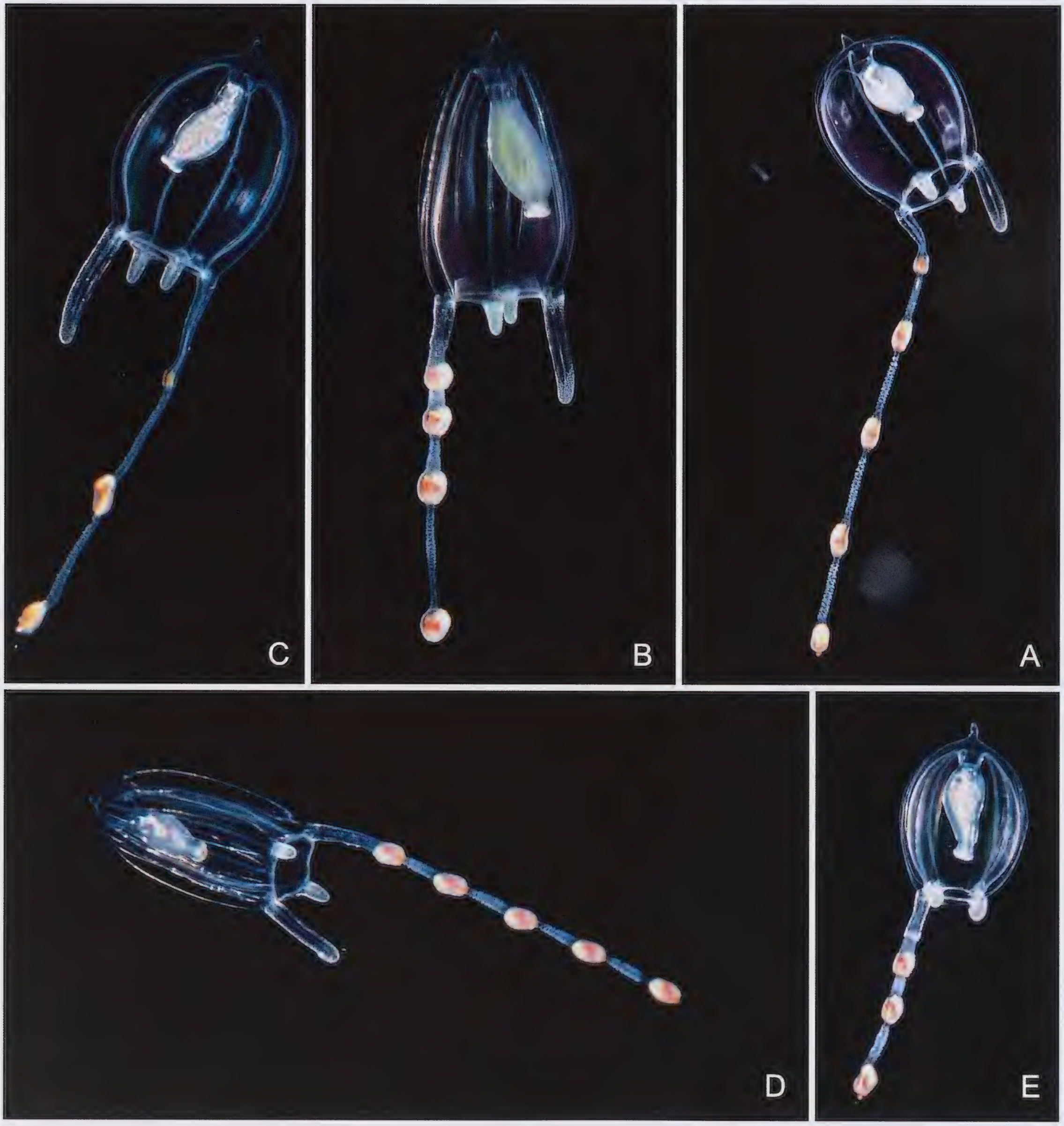


Fig. 26. *Corymorpha floridana* n. spec (A) Holotype, BFLA4371, bell height 3 mm. (B) 01-APR-2019; photographed but not collected; mature male, 2 mm. (C) 11-MAR-2020; photographed but not collected; 2 mm. (D) BFLA4363; bell height 2 mm. (E) BFLA4362; 2 mm; note that part of the long tentacle and the entire intermediate length tentacle are missing.

submitted as FU-014055; 4 mm bell. – 13-MAR-2020; 1 specimen photographed, not collected; 2 mm. – 16-MAR-2020; 2 specimens photographed, not collected; 2 mm.

Type locality: USA, Florida, 5.5-12 km east of Palm Beach; WGS84 26.70, -79.94 to 26.78, -79.94; depth 10 m.

Etymology: The name refers to the Florida Peninsula were the species was found.

Diagnosis: *Corymorpha* species with one long moniliform tentacle, one much shorter filiform tentacle opposite, and two tentacle stumps. Long tentacle with up to five orange, round to oblong nematocyst rings, including a terminal button. Bell with very small, pointed apical projection, no apical canal. Manubrium simple, on short gastric peduncle.

Description: Medusa with umbrella 2-3 mm high and about 1.6 mm wide (Fig. 26A-E), evenly bell-shaped, jelly relatively thin, not much thickened at apex, regularly with a small, pointed projection, not much varied in size. Manubrium on short gastric peduncle, spindle shaped, about half or somewhat more of the height of the subumbrella, mouth circular, with white rim. Gonads encircle nearly whole manubrium as relatively thin layer, without folds or perradial interruption. Four radial canals and circular canal thin, smooth. No tentacle bulbs or ocelli. Four tentacles of three types. One long tentacle, much extensible, contracted about two bell heights long, thick, only slightly tapering; nematocysts concentrated in three to five nematocyst rings, one knob in terminal position, rings more or less equidistant and well separated, shape round to oblong when tentacle extended, colour orange. Tentacle opposite the long tentacle about half the length of the bell-height, evenly thick, end rounded, without nematocyst buttons, with some nematocysts at base and at end. Other two tentacles short, length about 1/3 of filiform tentacle, conical, with scattered nematocysts.
Variation: the mid-length tentacle was missing in one specimen (Fig. 26E), otherwise morphology rather uniform.
Corymorpha floridana, like other *Corymorpha* species, has a rather distinctive zigzag swimming style due to its unbalanced tentacle arrangement.

16S Data: A blastn search in GenBank using the sole 16S indicated *Corymorpha nutans* as best match, although with only 88% identity. This species was followed by other *Corymorpha* and other Aplanulata species with similar low identify scores.

Remarks: We were unable to identify our material with any of the described *Corymorpha* species (Schuchert, 2020) and therefore introduce it here as a new nominal species. With its tentacle configuration it conforms with the scope *Euphysora* Maas, 1905, a genus synonymized with *Corymorpha* M. Sars, 1835 by Petersen (1990). Some authors continue to regard it as valid, *e.g.* Bouillon *et al.* (2006).
Corymorpha floridana n. spec. resembles three other species, but can easily be distinguished from them:
– *Corymorpha bigelowi* (Maas, 1905): has a long tentacle with adaxial nematocyst clasps and not in rings, also larger apical projection; Indo-Pacific distribution (Schuchert, 2010; Madkour *et al.*, 2019).
– *Corymorpha annulata* (Kramp, 1928): has a distinct apical canal, a larger apical projection, many more (up to 17) nematocyst rings and these much narrower and not round or oval; Indo-Pacific distribution (Kramp, 1968).
– *Corymorpha crassocanalis* (Xu & Huang, 2003): has a long tentacle with adaxial nematocyst clasps and not in rings, no apical canal, broad and indistinct apical projection, broad radial canals (coasts of China).
Although distinct, *Corymorpha floridana* n. spec. is a rather simple medusa from a genus with a much more complex polyp stage. There is thus a danger that more than one polyp could be found that produce the same medusa (e.g. as for many *Clytia* species) and the species will thus become unrecognizable. However, through the available 16S sequence data this problem is likely resolved. To our knowledge, there is only one polyp-based *Corymorpha* species that is endemic to the NW Atlantic, namely *Corymorpha pendula* L. Agassiz, 1862, but this species does not produce free medusae. The polyp of the medusa *Corymorpha bigelowi* was described by Sassaman & Rees (1978).

Order Leptothecata
Family Laodiceidae L. Agassiz, 1862
Genus *Laodicea* Lesson, 1843

Laodicea Lesson, 1843: 294, type species *Medusa crucigera* Gmelin, 1788 by monotypy.
Laodice Lesson, 1843: 294, invalid non-Latin name.
Octorhopalon von Lendenfeld, 1885: 919, type species *Octorhopalon fertilis* von Lendenfeld, 1885 by monotypy.

Diagnosis: Medusa with four simple radial canals; gonads along radial canals; with marginal cordyli, with or without marginal cirri, with adaxial ocelli, without statocysts.

Laodicea undulata (Forbes & Godsir, 1853)
Fig 27A-E

Laodicea undulata. – Schuchert, 2017a: 353, fig. 2A-C, redescription, complete synonymy.

Examined material: BFLA3797; 1 specimen; 13-OCT-2018; size 6 mm; preserved in alcohol for DNA extraction; 16S sequence MW528645. – BFLA3806; 1 specimen; 19-OCT-2018; preserved in alcohol for DNA

extraction; 16S sequence MW528646. – BFLA3812; 1 specimen; 20-OCT-2018; size 8 mm; preserved in alcohol for DNA extraction; 16S sequence MW528647. – BFLA3836; 1 specimen; 19-NOV-2018; size 6 mm; preserved in alcohol for DNA extraction; 16S sequence MW528648. – BFLA4126; 1 specimen; 06-JUN-2019; size 10 mm; has one branched radial canal, thus 5 radial canals in total; preserved in alcohol for DNA extraction; 16S sequence identical to MW528648. – 04-MAR-2019; 1 specimen photographed, with one radial canal joining another radial canal instead of manubrium, not collected.

Observations: *Laodicea* medusae with umbrella up to 10 mm wide, all individuals not fully grown; stomach quadratic, short, with four folded lips. Gonads contiguous with stomach and spreading along proximal half to 2/3 (depending on bell size and age) of widened radial canals (= basal stomach pouches or extensions), flat leaf-like, pendant, sinuous. Up to 100 tentacles; small tentacle bulbs that taper gradually into tentacle, bulb usually with an adaxial ocellus, usually one marginal cirrus between successive tentacles; usually one cordylus between successive tentacles.

16S Data: A blastn search in GenBank with the four obtained sequences gave always as best match one of the European *Laodicea undulate* sequences, although the similarities were rather low (92-95%). The haplotypes from Florida showed high divergence values of up to 10.6% (Table 1), while the three European haplotypes have only 0.5% bp differences. A maximum likelihood tree separated the sequenced into three distinct lineages (Fig. 28).

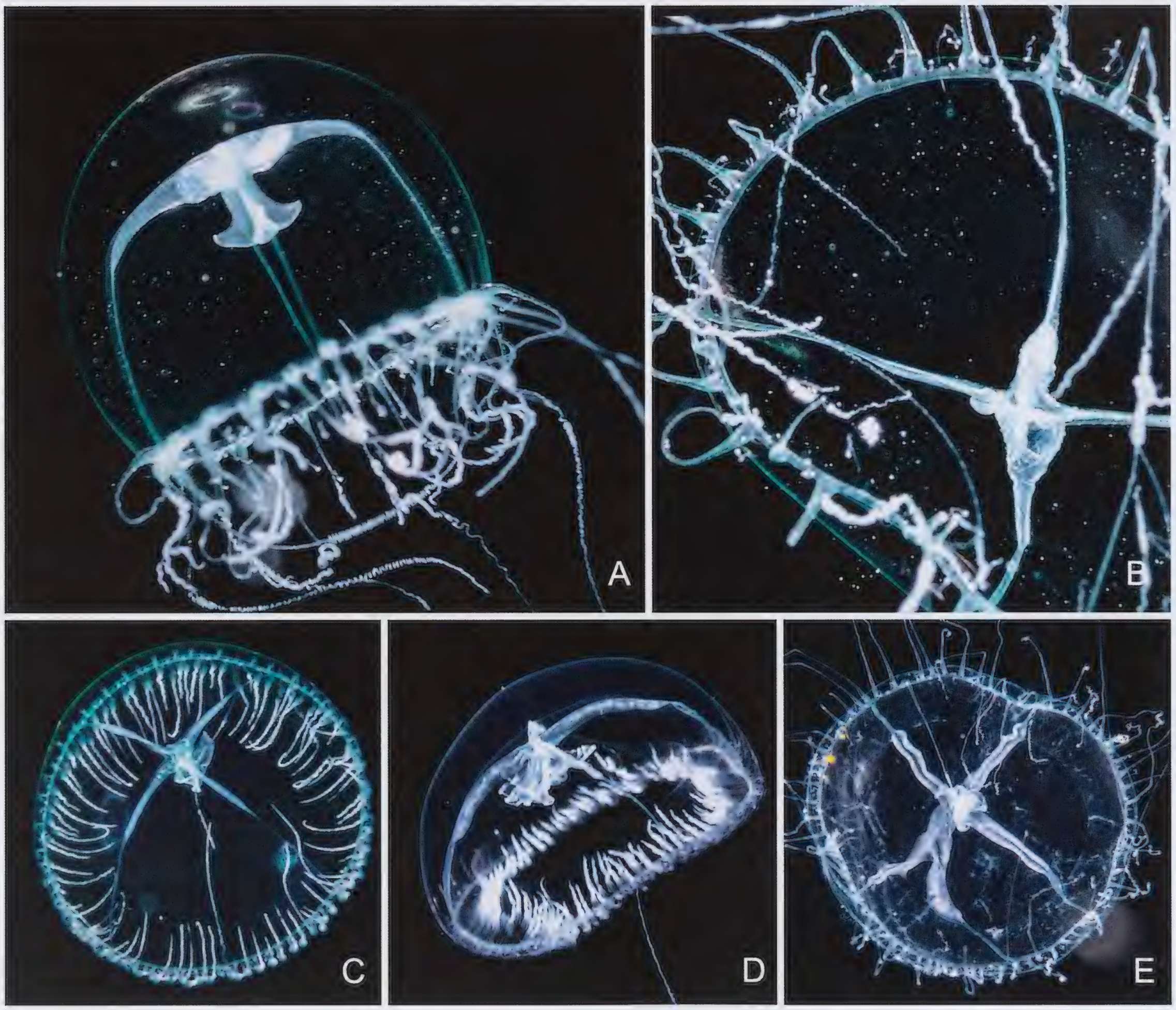


Fig. 27. *Laodicea undulata*, all not fully grown. (A-B) BFLA3836, size 6 mm, subadult. (A) Lateral view of whole animal, bell contracted and therefore higher than when relaxed. (B) Aboral view showing bell margin, cirri and cordyli are visible. (C) BFLA3836, size 6 mm. (D) BFLA3812, size 8 mm. (E) BFLA4126, size 10 mm, note the aberrant, branched radial canal.

Distribution: Eastern Atlantic and adjacent waters from Iceland and northern Norway to South Africa; western Atlantic from Nova Scotia to Tierra del Fuego; Mediterranean (Kramp, 1968). Some occasional records from the Indo-Pacific require a re-evaluation (Schuchert, 2017a). Type locality: The Minch, Scotland.

Remarks: It is arguable if the widened radial canals with the gonads (Fig. 27) should not better be interpreted as basal perradial extensions or pouches of the manubrium.

Although the animals of this study were morphologically not separable, some of their 16S sequences were very divergent, suggesting the presence of cryptic species (Fig. 28). *Laodicea undulata* has a complex synonymy. It includes also a nominal species of the NE Atlantic, namely *Laodicea calcarata* L. Agassiz, 1862 (see Agassiz, 1865), but this nominal species is currently not separable from *L. undulata* (comp. Cornelius, 1995; Schuchert, 2017a). Mayer (1900) described *Laodicea neptuna* from Florida. As it has only eight tentacles it

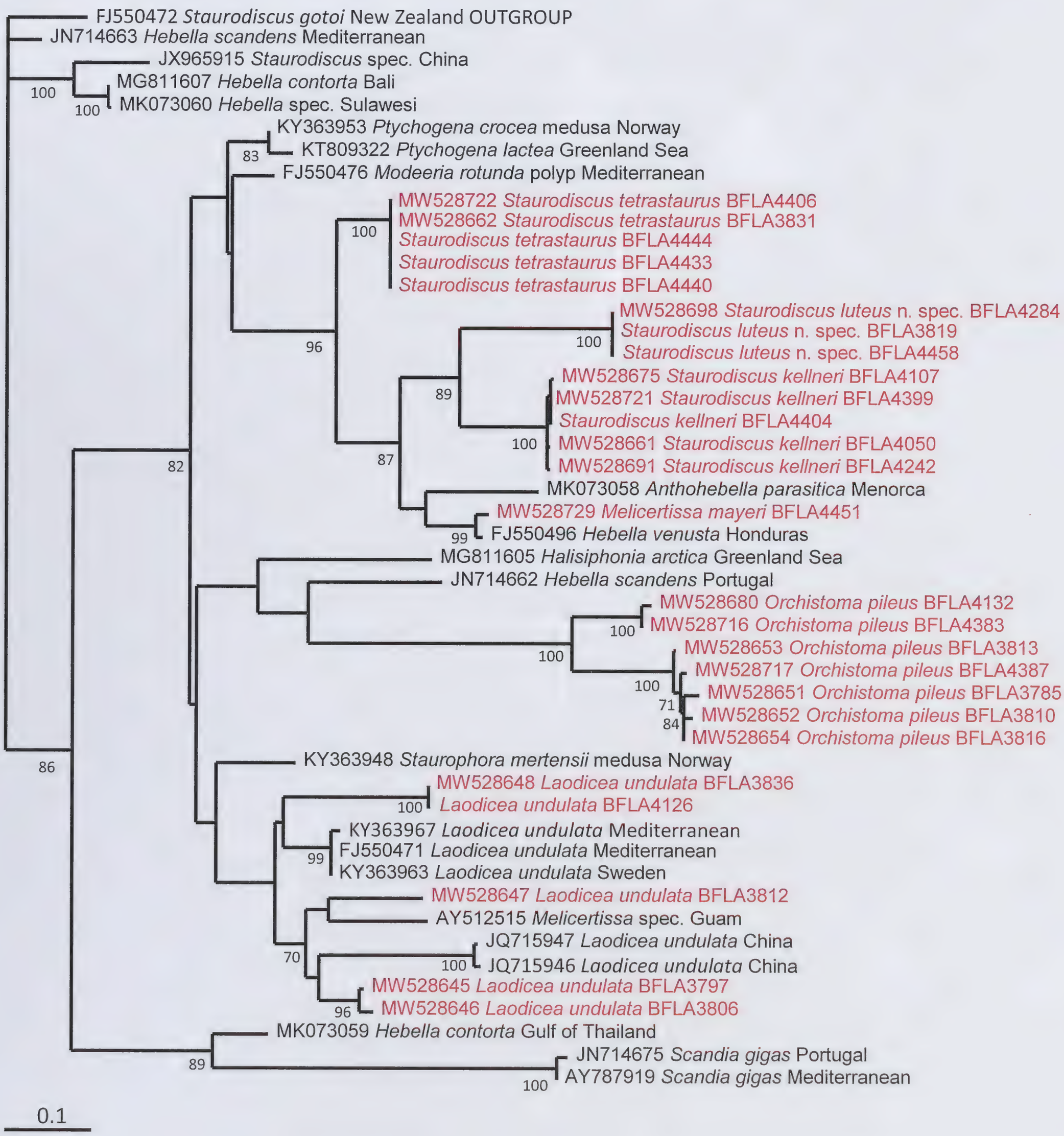


Fig. 28. 16S maximum likelihood phylogenetic tree of Laodiceidae, Hebellidae, and Orchistomatidae, obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). All sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Red labels are new sequences from this study.

cannot be one of the *Laodicea* observed here. Kramp (1959a) regarded it as a *species inquirenda*.

Family Hebellidae Fraser, 1912
Genus *Melicertissa* Haeckel, 1879

Melicertissa Haeckel, 1879: 135; type species *Melicertissa clavigera* Haeckel, 1879 by monotypy.
Melicertella Haeckel, 1879: 134; type species *Melicertella panocto* Haeckel, 1879 by monotypy.

Diagnosis: Medusae with eight unbranched radial canals; stomach with eight basal perradial stomach extensions, leaf-like; bulbs and cordyli with adaxial ocelli; with or without cirri. Hydroid *Hebella* like.

Remarks: See Uribe-Palomino *et al.* (2018: 26, table 1) for a synopsis of the species.

Melicertissa mayeri Kramp, 1959
Fig. 29A-C

Melicertissa clavigera. – Mayer, 1910: 210, pl. 24 figs 2-3. [not *Melicertissa clavigera* Haeckel, 1879]
Melicertissa mayeri Kramp, 1959a: 139, fig. 162, new name. – Kramp, 1961: 144. – Uribe-Palomino *et al.*, 2018: 26, table 1.
? *Lafoea venusta* Allman, 1877: 11, pl. 6 figs 3-4. [possible synonym]
? *Hebella venusta*. – Calder, 1991: 41, fig. 25. – Boero *et al.*, 1997: 39, species inquirenda. – Galea, 2010: 13, fig. 4E-G. – Calder, 2013: 17, fig. 5a. – Calder, 2019: 33, fig. 8a.

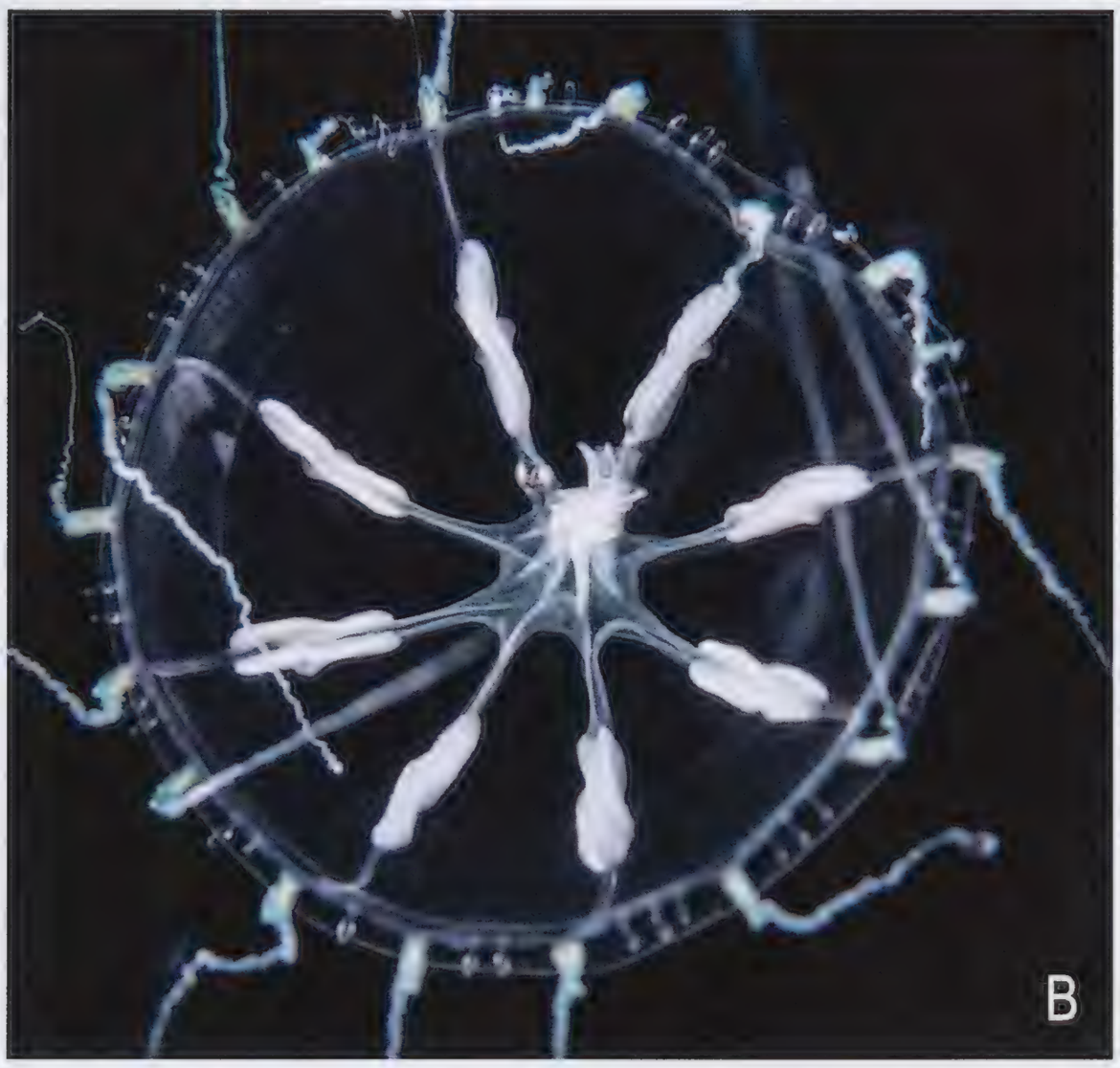
Examined material: BFLA4451; 1 specimen; 08-JUN-2020; size 10 mm; part preserved in formalin and deposited as UF-014062, part preserved in alcohol for DNA extraction; 16S MW528729.

Observations: *Melicertissa* medusa with nearly hemispherical bell, diameter 10 mm, apical jelly thickened. Manubrium relatively small, cross-section an eight-rayed star, mouth with eight simple lips, base star-shaped and widened, continued as eight basal perradial stomach extensions, leaf-like, replacing about 2/3 of radial canal, continued after this as thin, unbranched radial canal. Gonads on distal part of basal stomach extensions, flat and leaf-like on both sides of extension, occasional folds present (Fig. 29B). Eight perradial and eight interradial tentacles fully developed, three adradial small tentacles, total number thus 19. Tentacle bulbs conical to ovoid. Between each pair of tentacles 1-3 cordyli, totally about 35. Adaxial ocelli on circular canal opposite each tentacle bulband cordylus. Cirri absent. Mostly colourless, gonads white, sides of tentacle bulbs with green hue.

16S Data: A blastn search in GenBank with the obtained sequences gave a good match of 98.7% similarity with the sequence FJ550496 obtained from the hydroid *Hebella venusta* (Allman, 1877). The maximum likelihood tree also shows the close relationship (Fig. 28).

Distribution: Florida (Kramp, 1959a); ?Indian Ocean (Navas-Pereira & Vannucci, 1991; a single individual only). Type locality: USA, Florida, Dry Tortugas archipelago.

Remarks: Mayer (1910) identified *Melicertissa* medusae from Florida as *M. clavigera* Haeckel, 1879 despite them having 16 tentacles instead of 8 as for typical *M. clavigera*. He considered this as intraspecifc variation with possibly *M. clavigera* being a younger form. Nair (1951) questioned this, mainly based on the assumption that Haeckel described *M. clavigera* has having 24 cordyli at a size of 10 mm, while Mayer (1910) depicted his medusa with only 16 cordyli at a diameter of 7 mm. If Mayer's specimens were older and had more tentacles, then they should not have fewer cordyli (although they might have been lost, they break away easily). Kramp (1959a) adopted Nair's suggestion and introduced the new name *Melicertissa mayeri* for Mayer's specimens. However, both Nair and Kramp must have overlooked comments in Mayer (1910: 211) in which he described the variation of tentacle numbers and cordyli. Some interradial tentacles may be replaced by a cordylus (resulting thus in less than 16 tentacles). Some octants of the bell may have two tentacles and three cordyli, others had three tentacles and 2 cordyli. The number of tentacles and cordyli is thus variable and Mayer's (1910) conclusion that *M. clavigera* is conspecific with the Florida population is understandable and needs re-examination using genetic methods.
Our specimen had 19 tentacles and about 35 cordyli, deviating thus somewhat from the scope given in Mayer (1910) and Kramp (1959a). Only very few specimens of both *M. clavigera* and *M. mayeri* have been described so far and it is very likely that the intraspecific variation of the tentacle- and cordylus numbers has been underestimated. Therefore, we nevertheless identified the present medusa as *M. mayeri*.
The 16S sequence matched rather closely (1.3% base pair differences, Fig. 28) to a sequence obtained from the hydroid *Hebella venusta* (Allman, 1877) collected in Honduras and growing on the hydroid *Thyroscyphus marginatus* (Fig. 30). The type material of *Hebella venusta* came from Loggerhead Key, Florida. Recent descriptions of *Hebella venusta* are given by Galea (2010) and Calder (2013, 2019). It is a nominal species with very few diagnostic traits and Boero *et al.* (1997) are right considering it a *species inquirenda* as our current concept of it could include several species (viz. the same hydroid morphotype but producing different medusae). It is therefore not clear if the material from which the sequence FJ550496 was obtained corresponds really to the *H. venusta* at the type locality.



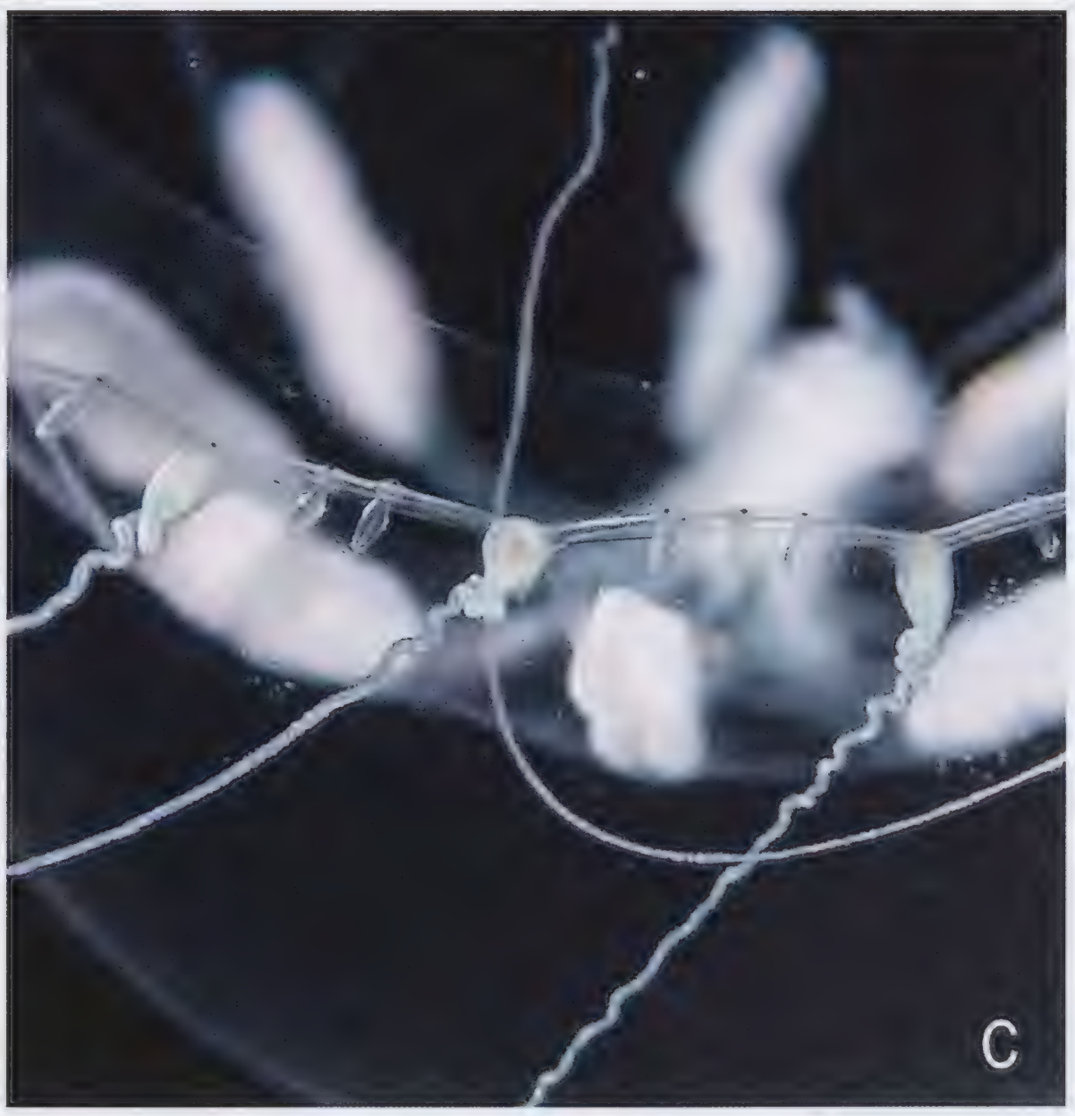


Fig. 29. *Melicertissa mayeri,* BFLA4451, size 10 mm. (A) Oblique view of whole animal. (B) Oral view. (C) Bell margin, note cordyli and ocelli.

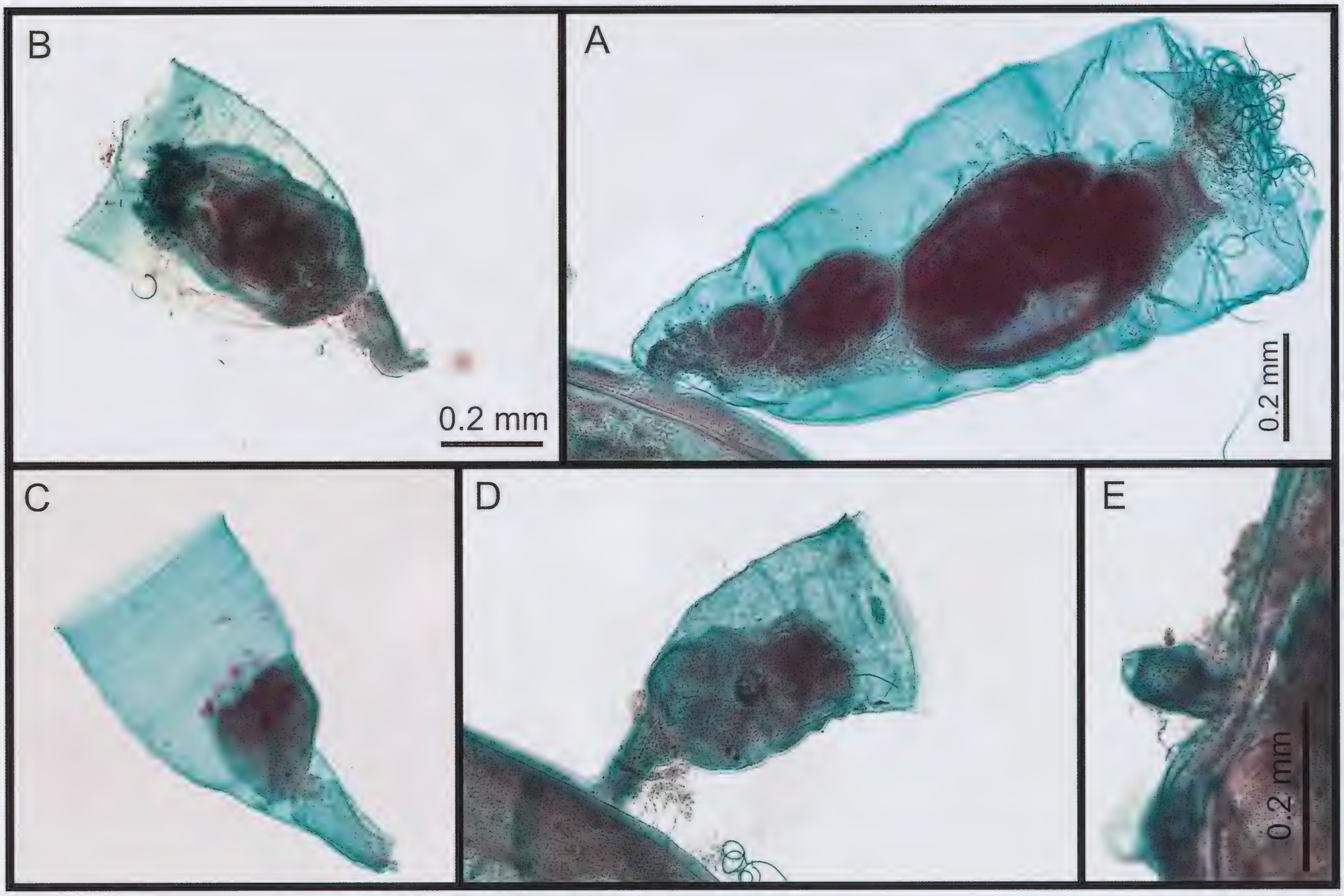


Fig. 30. Hydroid *Hebella venusta*, MHNG-INVE-0035476, from Honduras, stained slide preparation, voucher specimen of 16S sequence FJ550496. (A) Gonotheca with medusa buds, ocelli are faintly visible. (B) Hydrotheca with hydranth, rim with four shallow cusps. (C-D) Hydrothecae with smooth rim. (E) Unidentified structure resembling a nematotheca, but it could also be a rest of a broken caulus.

However, *Melicertissa mayeri* is clearly not a member of the Laodiceidae (Fig. 28) but must be transferred to the Hebellidae (comp. also Migotto & Andrade, 2000). According to the tree (Fig. 28) it appears even congeneric with *Staurodiscus*.

Genus *Staurodiscus* Haeckel, 1879

Staurodiscus Haeckel, 1879: 145, type species *Staurodiscus tetrastaurus* Haeckel, 1879 (Kramp, 1961: 147).
Staurodiscalma Haeckel, 1879: 145, type species *Staurodiscus tetrastaurus* Haeckel, 1879 by monotypy.
Staurodiscema Haeckel, 1879: 146, type species *Staurodiscus heterosceles* Haeckel, 1879 by monotypy.
Toxorchis Haeckel, 1879: 157, type species *Toxorchis arcuatus* Haeckel, 1879 by monotypy.
Staurodiscoides Uchida, 1927b: 165, type species *Staurodiscoides gotoi* Uchida, 1927 by monotypy.

Diagnosis: Medusa with 4 or more main primary radial canals, some or all branching one or more times, primary canal and some or all of the branches reaching circular canal; gonads on primary radial canals and branches; numerous tentacles and cordyli; with or without cirri; with or without ocelli.
Hydroid epizootic, *Hebella*-like; hydrothecae almost conical when growing on upper part of the host, cylindrical when growing on lower part of same host; asymmetrical to symmetrical; with everted margin, sharply or slightly oblique, with short to long, wrinkled or annulated pedicels; with membranous diaphragm (sometimes absent) and annular thickening; gonophores as free medusae; gonotheca as big or slightly bigger than hydrotheca, with four opercular flaps, on short pedicel, slightly undulated walls, truncated distally, tapering at base, containing up to three medusae (Bouillon *et al.*, 2006).

Remarks: See Kramp (1962) and Bouillon (1984b) for emended diagnosis and synopsis of the species. For the life cycle see Migotto & Andrade (2000).

Staurodiscus kellneri (Mayer, 1910)

Fig. 31A-H

Toxorchis kellneri Mayer, 1910: 229, pl. 28 figs 1-2. – Vanhöffen, 1913a: 421. – Bigelow, 1917: 306. – Bigelow, 1926: 54. – Kramp, 1959a: 141, fig. 167. – Kramp, 1961: 150.

Dipleurosoma brooksii Mayer, 1910: 227, fig. 118a-b, **nov. syn.**

Toxorchis brooksi. – Kramp, 1959a: 141, fig. 168b. – Kramp, 1961: 147.

Hebella furax. – Migotto & Andrade, 2000: 1873, figs 1-5. [? not *Hebella furax* Millard, 1957]

? *Toxorchis milleri* Bouillon, 1984b: 71, fig. 20.

? not *Staurodiscus kellneri.* – Bouillon *et al.*, 2004: 152, figs 82A-D.

Examined material: BFLA4050; 1 male; 01-APR-2019; size 20 mm; preserved in formalin (UF-013450) and small part in alcohol for DNA extraction; 16S sequence MW528661. – BFLA4074; 1 specimen; 11-APR-2019; size 13 mm; preserved in formalin (UF-013784) and small part in alcohol for DNA extraction; 16S sequence identical to MW528721. – BFLA4107; 1 specimen; 27-MAY-2019; size 10 mm, only 9 radial canals; preserved in formalin (UF-013794) and small part in alcohol for DNA extraction; 16S sequence MW528675. – BFLA4242; 1 specimen; 11-NOV-2019; size 7 mm; preserved in formalin (UF-013835, sample macerated, only debris left) and part in alcohol for DNA extraction; 16S sequence MW528691. – BFLA4399; 1 specimen; 17-MAY-2020; size 11 mm; preserved in formalin (UF-014041) and small part in alcohol for DNA extraction; 16S sequence MW528721. – BFLA4404; 1 specimen; 26-MAY-2020; size 8 mm; preserved in alcohol for DNA extraction; 16S sequence identical to MW528721. – BFLA4424; 1 specimen; 28-MAY-2019; size 9 mm; preserved in formalin (UF-014050) and small part in alcohol for DNA extraction; 16S sequence MW528726. – BFLA4452; 1 specimen; 08-JUN-2020; size 14 mm; preserved in formalin and deposited as UF-013450. – 30-MAY-2020; 1 specimen; photographed but not collected; 10 mm, 9 radial canals, juvenile.

Observations: Umbrella diameter 10-20 mm, hemispherical or slightly flatter than hemisphere, lateral jelly thin but gradually thickening towards apex, the latter moderately thick. Manubrium rather flat, mouth wide open or a short tube with variable number of folded lips, manubrium base much enlarged and drawn out star-like into up to 12 basal extensions which may branch into two or three radial stomach extensions and reaching almost to circular canal, continued as short radial canals (about 1/6 of bell radius) and these all connected to circular canal, no blind ending radial canals or stomach extensions, 16-19 radial canals. Branching pattern variable and irregular, some radial canals not branching. Gonads develop on lateral walls of stomach extensions, reaching from branching points to beginning of radial canals, colour pale reddish-brown or brown-yellow. Tentacles 23-32, with distinct ovoid marginal bulb, black ocellus on adaxial side where joined to umbrella. Marginal bulbs independent of radial canals. Between each pair of tentacles usually one, sometimes 2-3 (especially in smaller animals) elongate cordyli, cordyli with a few terminal nematocysts, at attachment site on adaxial side a black ocellus. No statocysts.

16S Data: The six 16S sequences obtained represented four haplotypes with only 0.16 to 0.5% base pair differences. In the maximum likelihood tree (Fig. 28) they are well separated from the other *Staurodiscus* species and also *Melicertissa* of this study.

Distribution: Florida and Gulf of Maine (Kramp, 1959a). Type locality: USA, Florida, Dry Tortugas archipelago. The Mediterranean occurrence given in Bouillon *et al.* (2004) is based on records of the hydroid *Hebella furax* Millard, 1957 and is most likely incorrect because the medusa is not known to occur in this well investigated area. It is by no means evident that the simple hydroid *Hebella furax* corresponds to *Staurodiscus kellneri* in all regions it has been reported. It is highly probable that *Hebella furax* represent a species complex (see also Remarks below).

Remarks: This is a rare medusa, only a few individuals have been described so far and the variation of the number of tentacles, radial canals, and the branching of the stomach extensions were not well known. Migotto & Andrade (2000) reared medusae released from a hydroid they collected in coastal waters of Brazil and identified as *Hebella furax* Millard, 1957. The resulting adult medusae were clearly identifiable as *S. kellneri,* although the authors hesitated somewhat with this identification, presumably because the branching pattern of the radial canals/stomach extensions were more variable than documented before. This trait was rather variable in our specimens too (Fig. 31A-G) and confirms the observations of Migotto & Andrade (2000). However, *Hebella furax* cannot simply be synonymized with *Staurodiscus kellneri. Hebella furax* [see Millard (1975) and also Boero *et al.* (1997)] was originally described from South Africa and is a widespread, rather simple hydroid offering few diagnostic features. It is very likely that it does not produce *S. kellneri* medusae over its whole distribution range, just like the "*Campanulina*"-type hydroids produce medusae belonging to different genera (see Schuchert *et al.*, 2017 for similar cases).

Staurodiscus brooksii (Mayer, 1910) (see description in Kramp, 1959a) from the Bahamas appears very similar to *S. kellneri.* The former has fewer tentacles and also fewer radial canals because four radial canals are unbranched. BFLA4399 had exactly this condition (Fig. 31F), while others like BLFA4050 (Fig. 31A) had it partially. Mayer (1910) described *S. brooksii* based on drawings made by

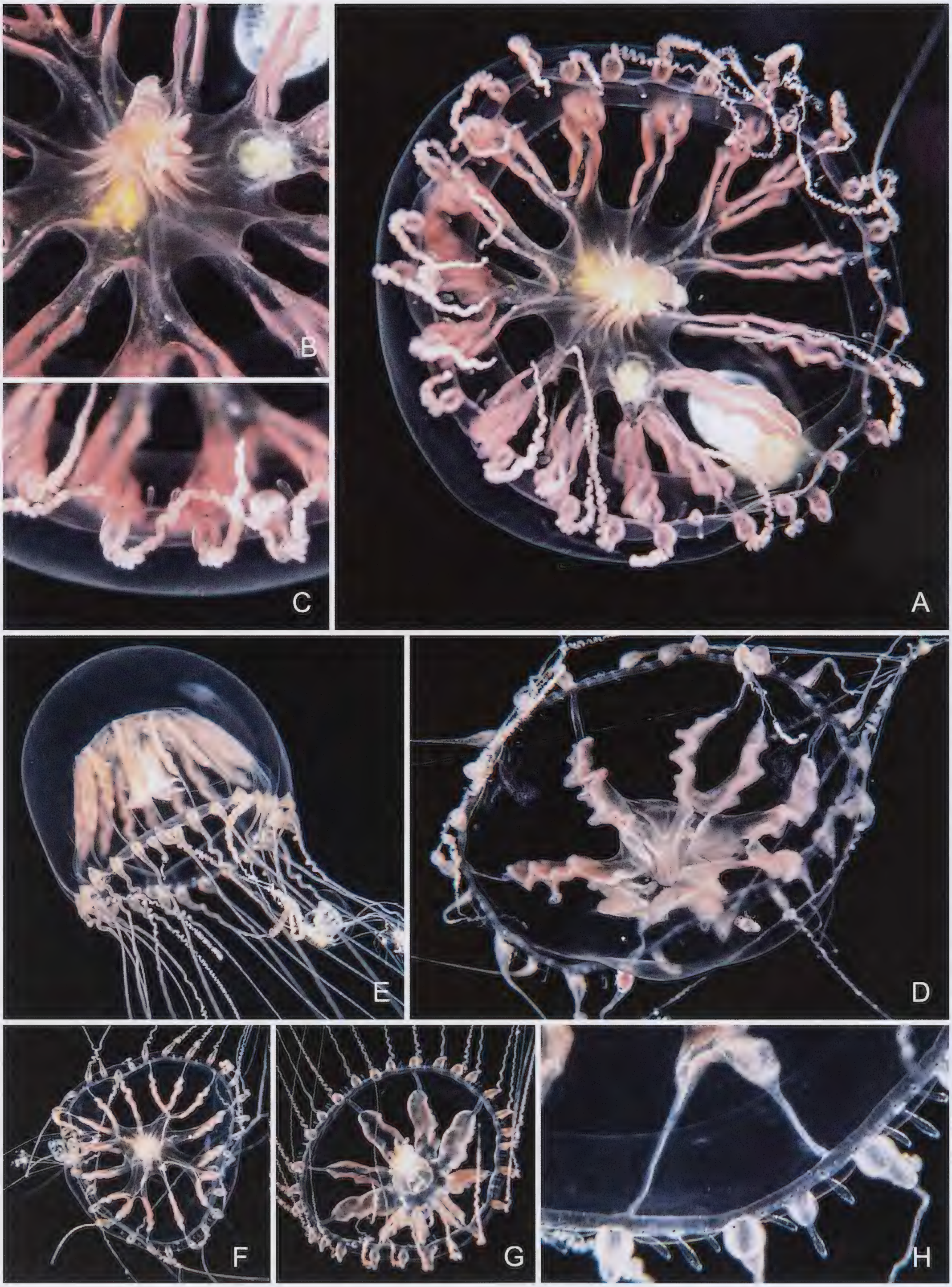


Fig. 31. *Staurodiscus kellneri*. (A-C) BLFA4050, size 20 mm. (A) Oral view, the oval, white body is a crustacean on the exumbrella. (B) Mouth part. (C) Bell rim, ocelli and cordyli are visible. (D) BFLA4107, size 10 mm, young animal with only nine radial canals reaching the circular canal. (E) BFLA4399, contracted bell, lateral view, size 11 mm. (F) BFLA4399, oral view, not all radial extensions are branched. (G) Animal photographed 12-OCT-2020, 10 mm, juvenile with 9 radial canals. (H) BFLA4242, bell diameter 7 mm, bell margin with bulbs and cordyli.

the late William K. Brooks of a medusa collected from Nassau, Bahama Islands. The drawing did not show ocelli, but they were probably overlooked by Brooks as they are rather small and not well visible (Fig. 31H). Kramp (1959a) pointed out that also the cordyli were also not mentioned in Mayer (1910), but they are shown in Mayer's figure (1910: 118aA). *Staurodiscus brooksii* must evidently be a younger stage of *Staurodiscus kellneri* and we regard both as conspecific. Both names were introduced in Mayer (1910), with *S. brooksii* appearing on page 227, *S. kellneri* on page 229. As the current ICZN does not enforce page precedence for synonymized names appearing in the same work, acting as first revisors we prefer to use the name *Staurodiscus kellneri* for the present species. It is the better and more precisely known nominal species and has been reported subsequently, while *S. brooksii* is incompletely described and has not been reported anymore (based on Kramp, 1961).

With the new data on the variability of the radial canals and their branching pattern in *Staurodiscus kellneri*, *S. milleri* (Bouillon, 1984b) becomes hardly distinguishable. They could well be conspecific. The only tangible difference remaining being the smaller size of *S. milleri* (up to 8.5 mm versus 10-20 mm). Although we think that both names should be synonymized, we hesitate to do so for biogeographic reasons. *Staurodiscus milleri* is only known from the Bismarck Sea, thus both nominal species have a very disjunct distribution.

Staurodiscus tetrastaurus Haeckel, 1879

Figs 32A-D

Staurodiscus tetrastaurus Haeckel, 1879: 145, pl. 9 figs 1-3. – Mayer, 1910: 214, pl. 22 figs 7-8, pl. 25 fig. 5, pl. 26 figs 10-11. – Uchida, 1927b: 167. – Menon, 1932: 14, pl. 2 figs 14, 19. – Nair, 1951: 60. – Kramp, 1959a: 140, fig. 165. – Kramp, 1961: 148. – Kramp, 1962: 321. – Kramp, 1968: 70, fig. 182. – Migotto & Andrade, 2000: table 6.

Staurodiscus heterosceles Haeckel, 1879: 146. **syn. nov.**

Examined material: BFLA3831; 1 specimen; 15-NOV-2018; size 7 mm; preserved in ethanol for DNA extraction; 16S sequence MW528662. – BFLA4406; 1 specimen; 26-MAY-2020; size 8 mm; preserved in ethanol for DNA extraction; 16S sequence MW528722. – BFLA4433; 1 specimen; 30-MAY-2020; size 5 mm; preserved in ethanol for DNA extraction; 16S sequence identical MW528722. – BFLA4440; 1 specimen; 07-MAY-2020; size 10 mm; preserved in ethanol for DNA extraction; 16S sequence identical to MW528662. – BFLA4444; 1 specimen; 07-MAY-2020; size 15 mm; part preserved in formalin and deposited as UF-014059, small part preserved in ethanol for DNA extraction; 16S sequence identical to MW528662. – 11-DEC-2017; 1 specimen photographed; juvenile, gonads not yet developed, not collected.

Observations: Bell hemispherical, 8 to 15 mm when mature, apical jelly about 1/3 of total height. Manubrium composed of central, cylindrical part and four basal, perradial extensions each with two lateral outgrowths in about middle of bell. Central part of manubrium tubular, with cruciform mouth opening drawn into four lips, margin slightly undulated. Basal, perradial extensions of stomach reaching almost to circular canal and thus length of radial canals to circular canal is short (1/4); stomach outgrowths relatively thick, giving off lateral diverticula in about the middle, these paired outgrowths opposite or not, oblique to radial axis or slightly curved, towards ends somewhat irregularly folded or undulating, not connecting to circular canal. Gonads in walls of stomach outgrowths. Mature animals with 23-30 tentacles and 1-3 cordyli between each pair of tentacles. Young animal with four perradial tentacles only and 7-9 cordyli per quadrant (Fig. 32A). Tentacles with conical bulbs. Small, inconspicuous ocelli present on adaxial side of tentacles bulbs and attachment sites of cordyli (Fig. 32F). Animal colourless or with greenish tint. Amphipods appear often to associate with the medusa (Fig. 32).

16S Data: The five obtained 16S sequences represented 2 haplotypes differing only one position (an insertion/deletion). In the maximum likelihood tree (Fig. 28) they are well separated from the other *Staurodiscus* species and also *Melicertissa* of this study. It is part of a well supported clade comprising the *Staurodiscus* species of this study and some Hebellidae.

Distribution: Canary Islands, Florida, Caribbean Sea, coast of Mozambique, coasts of India, Singapore, Taiwan Strait, Bismarck Sea (Kramp, 1959a, 1968; Bouillon 1978a, 1984b; Navas-Pereira & Vannuci, 1991; Zhang, 1999; Segura-Puertas *et al.*, 2003). Type locality: Atlantic Ocean, Canary Islands, near Lanzarote.

Remarks: Haeckel (1879) introduced two nominal *Staurodiscus* species, *S. tetrastaurus* and *S. heterosceles*, both collected at the same time and near Lanzarote Island. The former had 8-16 tentacles, 48 cordyli, and a bell diameter of 4-6 mm, the latter 8-32 tentacles, 40-80 cordyli, and a bell diameter of 6-8 mm [note that the figures in Kramp (1959a, 1968) depict a juvenile *S. tetrastaurus* with four tentacles, compare Fig. 32A]. Additionally, Haeckel distinguished both nominal species based on the branching pattern of the radial canals (= actually basal extensions of the manubrium, comp. Fig. 32A, E, G): *S. tetrastaurus* has opposite pairs, while they were not opposite in *S. heterosceles*. Haeckel (1879) also observed intermediate forms and explicitly expressed doubts that they are "*bona species*", but nevertheless named both forms [Haeckel used an artificial, typological species concept and did not distinguish biological species, comp. comments in Haeckel, 1879: XXV, 109]. Kramp (1962, 1968) too thought that both names refer likely to the same species.

One of our specimen (BFLA3831) was also intermediate as it had the size and tentacle numbers of *S. heterosceles,* but the outgrowths of the stomach had opposite side-branches (Fig. 32E). Others (Fig. 32G) had a variable branching pattern. The observed juvenile specimen (Fig. 32A) had three opposite and one alternate pairs of side-branches. It is thus quite clear that *S. tetrastaurus* and *S. heterosceles* must be regarded as conspecific, *S. tetrastaurus* being the valid name. Medusae identified as *Staurodiscus heterosceles* have – to our knowledge – not been recorded anymore since Haeckel's time.

Andrade & Migotto (1997) reared the initial stages of medusae released from a hydroid referable to *Hebella scandens* (Bale, 1888) and found that they resembled our *S. tetrastaurus.* Our 16S phylogeny (Fig. 28) also suggests a more close relationship to Hebellidae than to Laodiceidae. *Staurodiscus tetrastaurus* is the type species of the genus, thus decisive to which family the genus belongs.

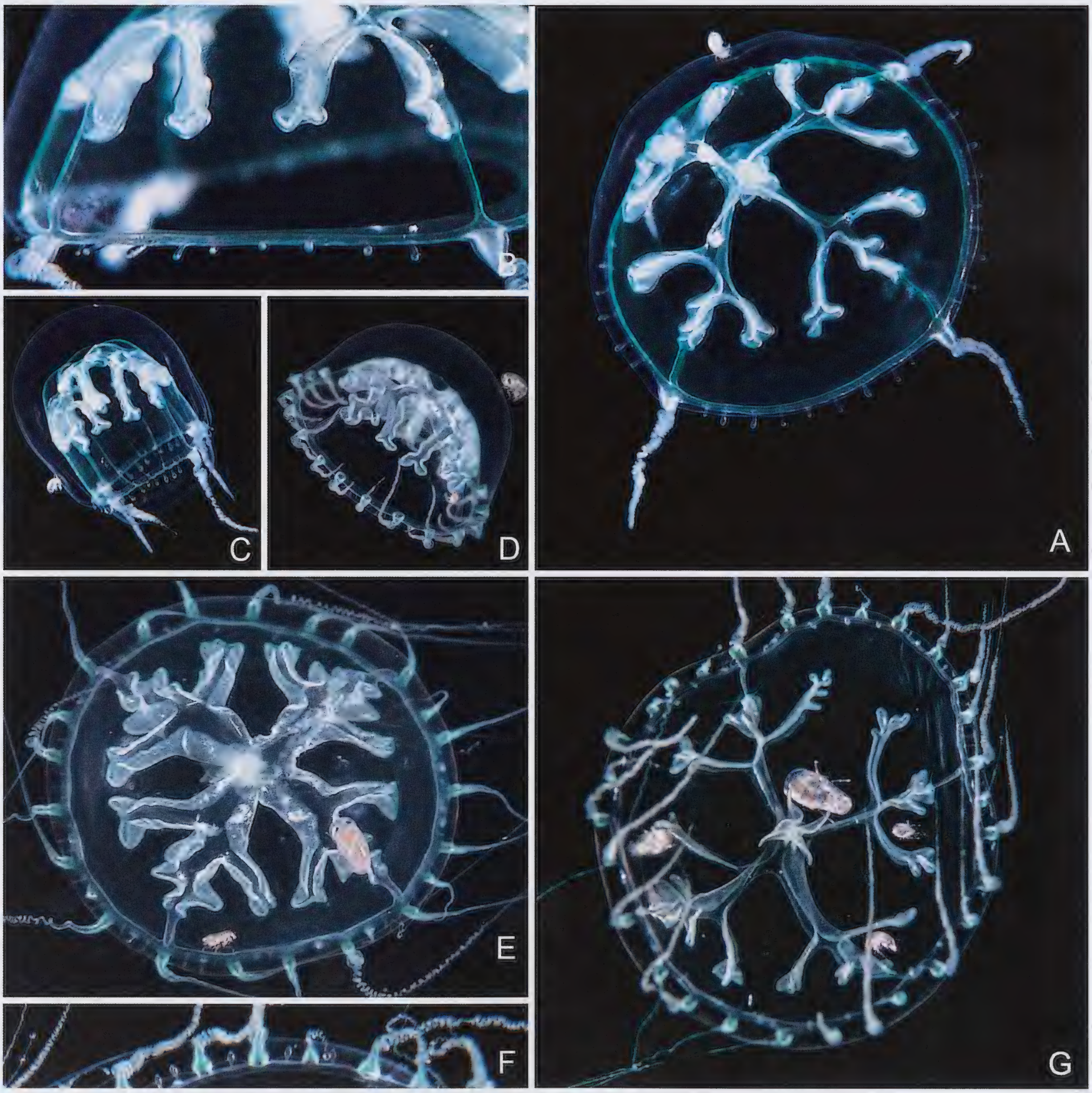


Fig. 32. *Staurodiscus tetrastaurus*. (A-C) Young animal observed 11-DEC-2017. (D-E) BFLA3831, size 7 mm. Some amphipods are associated with the animal. (F) BFLA4440, size 10 mm, bell margin seen from adaxial side, ocelli are barely visible. (G) BFLA4440, oral view, note variation of position of lateral diverticula.

Staurodiscus luteus n. spec.

Fig. 33A-H

Holotype: BFLA4284; 1 specimen; collected off Palm Beach, Florida, 06-DEC-2019; size 6 mm, ~32 tentacles; bell fragments preserved in formalin and deposited as UF-013842, fragment in alcohol used for DNA extraction (MHNG-INVE-0137382); 16S sequence MW528698.

Other examined material: BFLA3819; 1 specimen; 24-OCT-2018; size ~2.5 mm, ~36 tentacles; preserved in ethanol for DNA extraction; 16S sequence identical to MW528698. – BFLA4458; 1 specimen, no photos taken; 11-JUN-2020; size ~8 mm; preserved in ethanol for DNA extraction; 16S sequence identical to MW528698. – 06-MAY-2017; 1 specimen photographed; 8 mm; not collected. – 26-JUL-2018; 1 specimen photographed; size ~5 mm ~38 tentacles; not collected. – 11-APR-2019; 1 specimen photographed; damaged, 8 mm, ~24 tentacles; not collected. – 27-MAY-2019; 1 specimen photographed; juvenile, ~2 mm, ~9 tentacles; not collected. – 27-MAY-2019; 1 specimen photographed; juvenile, 2.5 mm, ~6 tentacles; not collected. – 17-MAY-2020; 1 specimen photographed; ~4 mm, ~24 tentacles; not collected. – 13-JUN-2020; 1 specimen photographed; 5 mm, ~17 tentacles; not collected.

Type locality: Atlantic Ocean, USA, Florida, approximately 6.5 km east of Palm Beach, WGS84 rectangle between 26.70, -79.94 and 26.78, -79.94, occurrence depth 8-10 m.

Diagnosis: Similar to the sympatric *Staurodiscus kellneri*, but smaller (<10 mm), with intensively yellow colour of stomach and its radiating extensions, and marginal bulbs; more radial canals (up to 30 and more) due to more branching, stomach extensions narrower, radial canals broader.

Description: *Staurodiscus* medusa with bell somewhat flatter than hemisphere, largest diameter observed 8 mm, apical jelly thick, about half the umbrella height (Fig. 33D). Conspicuous, opaque, intensively golden-yellow colour of stomach, radial canals and marginal bulbs, colour fading in peripheral regions of radial canals; colour is partially preserved in alcohol. Stomach wide, up to half the diameter of the subumbrellar diameter, shallow, base irregularly star-shaped, turning into basal stomach extensions which taper radially and branch irregularly 0 to 3 times and changing gradually into 30 to 40 radial canals which all reach the circular canal, radial canals very short. Gonad tissue (gametes) could not be seen in the preserved material, thus animals likely not reproductive. About 24 to 38 tentacles, long, contracted tightly coiled, their bulbs ovoid, clearly separated from rest of tentacles. Marginal bulbs positioned independently of radial canals. Usually only one cordylus between pairs of tentacles, also in younger individuals, sometimes cordylus on a marginal bulb without tentacle. Small, brown ocellus on base of adaxial side of bulb or on radial canal at attachment sites of cordylus. On aboral side of manubrium the cross-like marks of an original state with only four radial canals can be seen (Fig. 33E). Branching of the radial stomach extensions must occur early in development. Amphipods appear occasionally to associate with the medusa.

Etymology: The Latin adjective *luteus* means yellow and refers to the striking yellow colour of this medusa.

16S Data: The three 16S sequences obtained in this study were all identical. *Staurodiscus kellneri* haplotypes have about 9% base pair differences to the one of *S. luteus*. The two species are clearly separated in the maximum likelihood tree (Fig. 28).

Distribution: Known from type locality only.

Remarks: The opaque, yellow or golden-yellow colour renders *S. luteus* rather conspicuous (Fig. 33), although it resembles otherwise *S. kellneri* and *S. milleri* (Bouillon, 1984b). The latter has about the same size and is thus even more similar. The radial canals are more branched in *S. luteus*, resulting in 30 to 40 canals, while *S. milleri* has up to 18. Bouillon (1984b) usually also observed living animals for his studies in the Hansa Bay and he would certainly have noted any conspicuous colour as it is present in *S. luteus*. We therefore assume that *S. milleri* was not pigmented.
It is though possible that formalin preserved material – which loses colours after some time – has previously been mis-identified as *S. kellneri* in the western Atlantic. Both species can be separated based on their size, branching patterns of the radial canals, and proportions. The identification is more secure if 16S data are used.

Family Orchistomatidae Bouillon, 1984
Genus *Orchistoma* Haeckel, 1879

Orchistoma Haeckel, 1879: 138; type species *Mesonema pileus* Lesson, 1843 (Kramp, 1961).
Tetracannota Mayer, 1900: 46; type species *Tetracannota collapsum* Mayer, 1900 by monotypy.

Diagnosis: Medusa with short manubrium on large gastric peduncle; mouth with 8-30 sinuous or crenulated lips; eight or more radial canals, simple, ramified, or in groups of four. Up to 64 marginal tentacles; no marginal cirri, but with thin, filiform, tentaculiform structures devoid of marginal bulbs; gonads usually on proximal parts of radial canals; numerous adaxial ocelli; without statocysts, without cordyli, without excretory pores or papillae.
Hydroid phase unknown.

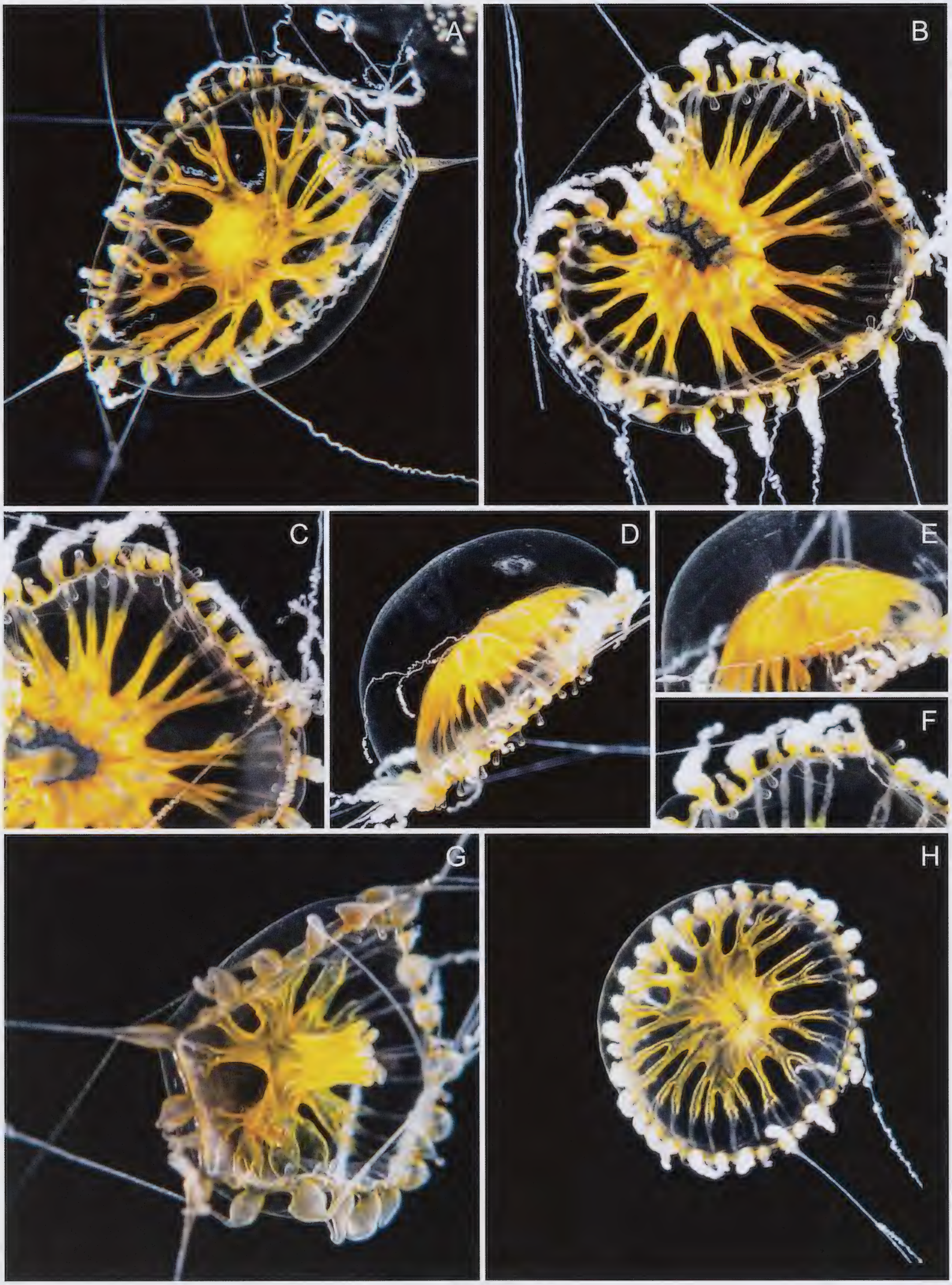


Fig. 33. *Staurodiscus luteus* n. spec. (A) Holotype, BFLA4284, 6 mm diameter, oblique view on oral side. (B-F) BFLA3819, size 2-3 mm. (B) Oral view. (C) Oral view. (D) Lateral view. (E) Oblique view on aboral part, note cross-shaped mark of original radial canals. (F) Bell margin from oral side, cordyli and ocelli are visible. (G) Juvenile, 4 mm, oral view, photographed 17-MAY-2020. (H) Photo taken 26-JUL-2018, aboral view.

Orchistoma pileus (Lesson, 1843)

Figs 34A-F & 35A-G

Mesonema pileus Lesson, 1843: 317, pl. 6 fig. 1.
Orchistoma pileus. – Haeckel, 1879: 139. – Kramp, 1959a: 139, fig. 163. – Kramp, 1961: 144. – Segura-Puertas *et al.*, 2009: 376. – Bouillon, 1984b: 90. – Gershwin *et al.*, 2010: table 7.
Orchistoma steenstrupii Haeckel, 1879: 139, pl. 15 figs 3-5. – Mayer, 1910: 211, pl. 25 figs 1-4. – Kramp, 1955a: 157, re-examination of type specimens, synonym.
Orchistoma agariciforme Keller, 1884: 418, pl. 21 figs 1-3. **n. syn.**
Orchistoma agariciforme. – Kramp, 1959a: 140. – Kramp, 1961: 144. – Bouillon, 1984b: 88, figs 29-30, redescription. – Bouillon *et al.*, 2004: 170, fig. 91E. – Gershwin *et al.*, 2010: table 7.
Tetracannota collapsum Mayer, 1900: 46, pls 7-8 figs 14-16. **n. syn.**
Dipleurosoma collapsum. – Mayer, 1910: 226, pl. 27 figs 1-3 & 7. – Kramp, 1961: 134. – Goy, 1979: 274, fig. 11. – Kramp, 1959a: 132, fig. 147.
Dipleurosoma collapsa. – Vanhöffen, 1913a: 420.
Orchistoma collapsum. – Bouillon, 1984b: 90, genus transfer. – Pagès *et al.*, 2006: 373, fig. 7A-C. – Gershwin *et al.*, 2010: table 7.

Examined material: BFLA3785; 1 specimen; 20-SEP-2018; size 12 mm; preserved in ethanol for DNA extraction; 16S sequence MW528651. – BFLA3810; 1 specimen; 20-OCT-2018; size 18 mm; preserved in ethanol for DNA extraction; 16S sequence MW528652. – BFLA3813; 1 specimen; 20-OCT-2018; size 20 mm; preserved in ethanol for DNA extraction; 16S sequence MW528653. – BFLA3816; 1 specimen; 20-OCT-2018; size 10 mm; preserved in ethanol for DNA extraction; 16S sequence MW528654. – BFLA4132; 1 specimen; 11-JUN-2019; size 34 mm; preserved in ethanol for DNA extraction; 16S sequence MW528680. – BFLA4183; 1 specimen; 12-AUG-2019; size 26 mm; preserved in formalin and deposited as UF-013823, no alcohol sample. – BFLA4383; 1 specimen; 09-MAY-2020; size 15 mm; part preserved in formalin and deposited as UF-014033, small part preserved in ethanol for DNA extraction; 16S sequence MW528716. – BFLA4387; 1 specimen; 09-MAY-2020; size 18 mm; part preserved in formalin and deposited as UF-014035, part preserved in ethanol for DNA extraction; 16S sequence MW528717. – 9 specimens, photographed but not collected; dates 10-APR-2019, 26-MAY-2020, 05-MAY-2017, 17-OCT-2017, 28-JUN-2018, 26-MAR-2019, 07-MAY-2019, 20-MAY-2019, 17-MAY-2020; sizes 15-30 mm.

Observations: Medusa bell diameter 10 to 34 mm when mature, almost hemispherical or somewhat shallower (Fig. 34A, D), evenly rounded exumbrella, mesoglea thick, jelly at apex about 2/5 of total height; with thick, tapering gastric peduncle that protrudes through velar opening. Velum broad. Stomach complex, base in centre H- or cross-shaped (Fig. 35A, D), then subdividing dichotomously or irregularly into elongate diverticula attached to the distal part of the gastric peduncle, walls of diverticula contain gonads and are continued on gastric peduncle as radial canals (Fig. 35A-D). Stomach wall follows the branching of the diverticula, mouth opening with complexly folded rim, mouth rim corners at position of diverticula drawn out into lips of variable length, 10 to 16 lips more elongated, sometimes also absent due to apparent damage and subsequent healing (Fig. 35F). Usually several radial canal in formation (Fig. 35E) and not reaching circular canal. Circular canal broad. Along circular canal on adaxial side numerous dark ocelli, not correlated with tentacle positions. 16 to 29 tentacles, extensible but also able to contract to short length (Fig. 34F), tentacles not in phase with the radial canals, with distinct, ovoid tentacular bulbs that taper rapidly into tentacles, bulbs divided bilaterally by a more transparent tissue in median line (Fig. 34C). Between each pair of tentacles 4 to 12, usually around 5 to 6, short thin tentacles (Fig. 34C), these secondary tentacles arise from circular canal, proximal half adnate to or embedded in umbrella, free part with nematocysts, contractile. Colours: stomach and diverticula with gonads can be brown-yellow in some specimens (Fig. 35B, E, F), otherwise whitish or with a yellow hue (Fig. 35D, G).

16S Data: The seven haplotypes found showed high divergence rates (Table 1). The sequences form a monophyletic group in the maximum likelihood tree (Fig. 28) but fell into two well separated subclades with relatively high divergence (up to 8.1%, Table 1), while the differences within the subclades are low.

Distribution: Western Atlantic from Maine (Pagès *et al.*, 2006) to Brazil (Goy, 1979), but mainly Bahamas, Florida and Caribbean (Haeckel, 1879; Vanhöffen, 1913a; Mayer, 1910; Kramp, 1959a), Gulf of Mexico (Segura-Puertas *et al.*, 2009), also Mediterranean (Bouillon, 1984b) and coast of Western Africa. Type locality: West Africa (Haeckel, 1879).

Remarks: Although the 16S data showed that our material separates in two lineages that might qualify as two distinct species (Table 1, Fig. 28), we referred all our samples to *Orchistoma pileus*.
Orchistoma pileus was first described by Lesson (1843), presumably based on a specimen from western Africa (as "mers d'Afrique ?"). Lesson's drawing was rather simple, but the species is recognizable. He did not show the small tentacles and there are about 30 normal tentacles or their bulbs depicted. Haeckel (1879) restricted the type locality to Western Africa and described concomitantly *O. steenstrupi* based on material from Cuba. The type material of *O. steenstrupi* was later re-examined by Kramp (1955a) and referred to *O. pileus* as it matched Mayer's (1910) description of this species. Mayer (1910) had material from the Bahamas and Tortugas. Kramp

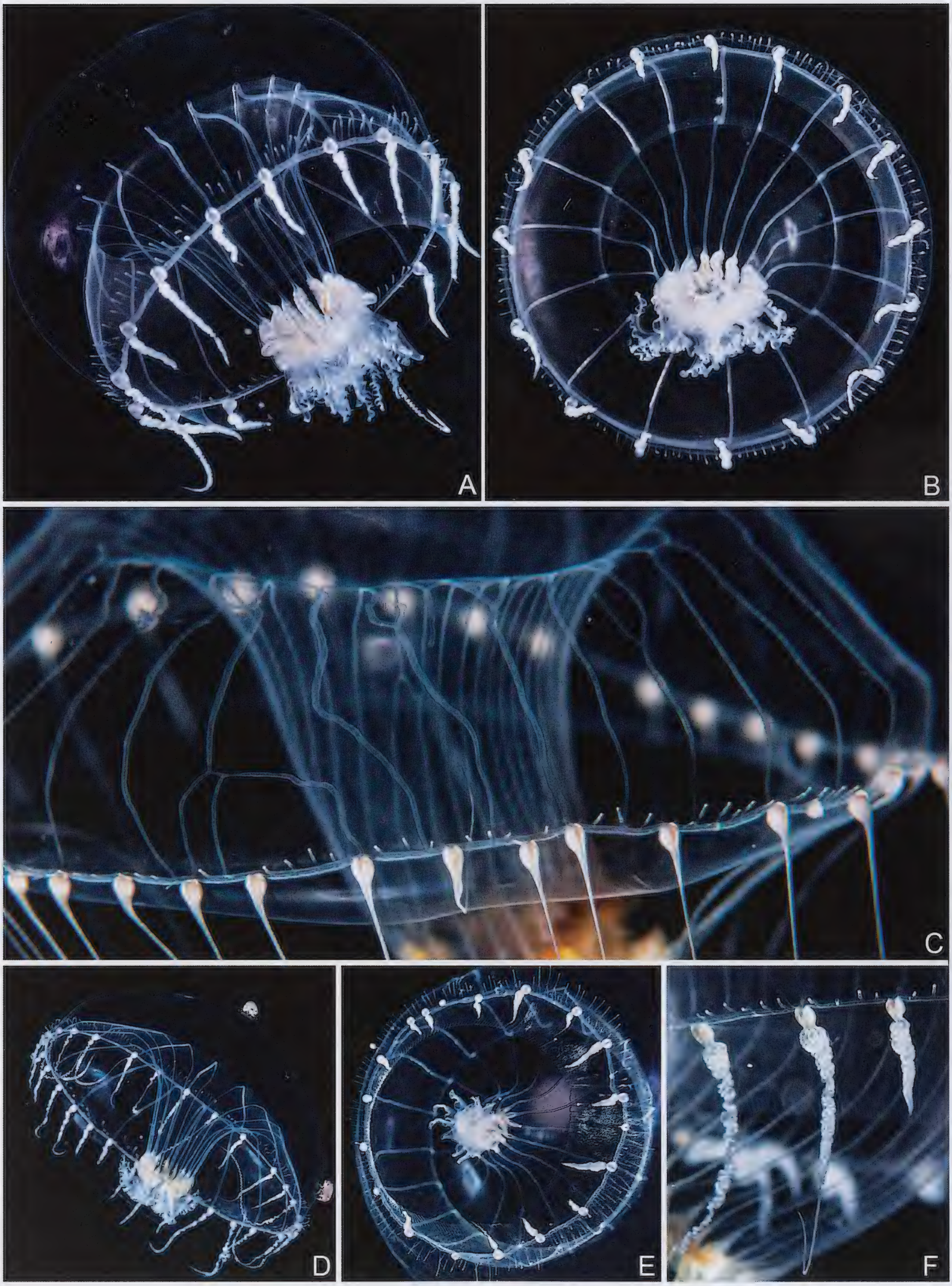


Fig. 34. *Orchistoma pileus*. (A-B) BFLA3785, bell diameter 12 mm, female. (C) BFLA4183, bell diameter 26 mm, bell margin of a mature animal, note irregular radial canals, likely due to healed damage. (D) BFLA3810, bell diameter 18 mm, male. (E) BFLA3813, bell diameter 20 mm. (F) BFLA4132, note curling of long tentacles.

Fig. 35. *Orchistoma pileus*. (A-D) Stomach details. (A) Young animal without gonads, *O. collapsum* stage, oral view, photo 10-APR-2019. (B) BFLA4183, mature female, bell diameter 26 mm, reticulate radial canals are likely due to a healed damage. (C) BFLA3785, bell size 12 mm, subadult female. (D) BFLA3810, bell diameter 18 mm, male, view from aboral side, note branching of radial canals (stomach diverticula), originating from a H-shaped figure, compare to A. (E) BFLA4383, size 15 mm. (F) BFLA4132, size 34 mm, manubrium likely damaged and in process of regeneration. (G) BFLA4387, size 18 mm.

gives the tentacle number as 64, which must be meant as a maximal number because the type specimen of Lesson had only 30.

Tetracannota collapsum was described by Mayer (1900) using medusae from the Tortugas and Bahamas. Despite the strong resemblance to *Orchistoma,* he placed it in a separate genus because it had visibly branched radial canals. His animals were mature but had only 16 tentacles at a size of 7 mm and only 8 manubrial lips. Mayer's branched radial canals are actually the same structure as here described for the stomach diverticula, only that the radial canals showed a grouping into four sets close to the manubrium, but more distally they are evenly distributed (comp. Fig. 35A). Later, Vanhöffen (1913a) found Mayer's species in the West Indies and noted that it is more variable than given in Mayer. Vanhöffen found them to have 16 manubrial lips beginning at a size of 3 mm.

Another nominal species resembling *O. pileus* was described by Keller (1884) as *Orchistoma agariciforme.* He had a single mature medusa from the Mediterranean with only 7 manubrial lips, but which was otherwise similar to *O. pileus*. Bouillon (1984b) described more specimens of *O. agariciforme* from the Mediterranean and considerably widened its morphological scope, notably he observed that the number of the manubrial lips was usually 16. Bouillon concludes that *O. agariciforme* is very close to both *O. pileus* and *O. collapsum.* He gives as distinguishing traits that in *O. collapsum* the radial canals remain in four groups near the manubrium even in adults and it has shorter manubrial lips. *Orchistoma pileus* differs by attaining a larger size of up to 30 to 40 mm, with up to 32 manubrial lips and radial canals as well as up to 64 marginal tentacles.

Gershwin *et al.* (2010) favoured splitting and retention of all these nominal species, even of *O. steenstrupi*, but used outdated values for *O. agariciforme* in their table.

The material we examined in this study was very variable and referable to either *O. pileus* and *O. agariciforme* and we think these names should be synonymized, including also *O. steenstrupi* and *O. collapsum*.

While we had no specimen that exactly matched *O. collapsum* as described by Mayer (1900, 1910), BFLA4383 (Fig. 35E) comes close to it in terms of tentacle and lip numbers. We nevertheless think that this nominal species was based on growth stages of *O. pileus*. Gonads mature in *O. pileus* at a size of less than 12 mm bell size (Fig. 34A) and the medusa continues its growth and the multiplication of radial canals and tentacles. Manubrial lips numbers and sizes are variable, usually there are about 16 somewhat longer lips. The lips can be damaged and regenerated and their number is not a reliable diagnostic feature (Fig. 35F). In general *O. pileus* appears as a rather variable species, mostly due to a long growth and different developmental stages.

This synonymy appears to be to some degree in conflict with the DNA data obtained in this study because the 16S sequences separate into two distinct lineages, although they are sister lineages (Fig. 28). We could not find convincing morphological traits that would allow to identify the lineages, except that in one the manubrium and gonads are brownish-yellow while in the other they are whitish (compare Fig. 35E & 35F versus 35G). BFLA4383 (Fig. 35E) was also in this "yellow" clade and was mentioned above as being close to the morphotype of *O. collapsum*. However, the other sample from this "yellow" clade (BFLA4132, Fig. 35F) is referable to *O. pileus*.

At this stage we cannot resolve the problem of the two lineages. The difference in colour could also be a random result due to low sample numbers. If it can be confirmed by a more detailed genetic analysis of more samples that indeed two species are involved, the two lineages are likely not separable so that they correspond to the nominal species synonymized here.

The high genetic subdivision is reminiscent to the one observed above for *Zancleopsis dichotoma* and *Laodicea undulata*.

Wuvulidae new family

Diagnosis: Medusa with more than four radial canals, sometimes partially ramified; tentacle bulbs and atentaculate bulbs with lateral sac-like appendages; large adaxial excretory papillae on marginal tentacular bulbs. Gonads on radial canals. No ocelli, no statocysts. Hydroid unknown.

Remarks: Bouillon *et al.* (1988b) when introducing the genus *Wuvula* included it in the family Laodiceidae based on the assertion that the appendages of the marginal bulbs resemble cordyli. Pendant cordyli (*e.g.* Fig. 29C) are typical for the Laodiceidae, but they also occur in the Hebellidae. They occur mostly on the bell margin, but may also be placed on marginal bulbs. The hollow appendages in *Wuvula* (Fig. 36F) are clearly not cordyli and also their paired position on the side of bulbs is not known for cordyli in the Laodiceidae. The genus must thus be removed from the Laodiceidae. *Wuvula* lacks ocelli, statocysts, and cordyli and could be related to the Melicertidae Agassiz, 1862 which also lack them. The absence of statocysts and cordyli is, however, likely a plesiomorphy and not suitable for postulating a relationship. Moreover, the 16S data of *W. ochracea* did not indicate relationship to any group (results not shown, but see below).

We therefore propose that the genus is accommodated in a new family Wuvulidae. Its diagnosis is given above and taken from the genus diagnosis.

Genus *Wuvula* Bouillon, Seghers & Boero, 1988

Wuvula Bouillon, Seghers & Boero, 1988b: 247; type species *Dipleurosoma ochraceum* Mayer, 1910 (see below).

Diagnosis: With the characteristics of the family.

Remarks: Bouillon *et al.* (1988b) did not select a type species for this genus. *Dipleurosoma ochraceum* Mayer, 1910 is therefore here designated as type species of the genus.

Wuvula ochracea (Mayer, 1910)

Fig. 36A-I

Dipleurosoma ochraceum Mayer, 1910: 226, pl. 29 figs 1-2. – in part Vanhöffen, 1913a: 421, not fig. A. – Kramp, 1959a: 132, fig. 146. – Kramp, 1961: 134.

Wuvula ochracea. – Bouillon, Seghers & Boero, 1988b: 248, new combination.

Examined material: BFLA4361; 1 specimen; 13-MAR-2020; size 3.5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528713. – BFLA4372 and BFLA4373; 16-MAR-2020; 1 specimen that split into 4 individuals of 3 mm, and some fragments; preserved in formalin and deposited as UF-014027 and UF-014028, fragments in alcohol for DNA extraction; 16S sequence identical MW528713. – BFLA4392; 1 specimen; 17-MAY-2020; size 4 mm; preserved in alcohol for DNA extraction; 16S sequence identical MW528713. – BFLA4470; 1 specimen; 17-JUN-2020; size 3.5 mm; preserved in alcohol for DNA extraction; 16S sequence identical MW528713. – 1 specimen photographed 04-JUN-2019, not collected; size 2.5 mm. – 1 specimen photographed 16-MAR-2020, not collected; size 4 mm.

Observations: Medusa 2.5 to 4 mm in diameter, bell flatter than hemisphere when relaxed, jelly relatively thin, velum very broad. Manubrium rather small, star-shaped in cross-section, mouth with about 6 corners drawn out into lips, mouth rim with no or only few folds. Six radial canals reaching circular canal, in addition up to 5 incomplete, thin radial canals originating from manubrium which do not reach circular canal. Complete radial canals with swelling at about 1/3 distance from manubrium, presumably the place where gonads will develop. Up to 14 relatively short and thin tentacles, all with a small, whitish marginal bulb; additionally up to 55 small, rudimentary bulbs without tentacles. All marginal bulbs with a laterally attached pair of large, club-shaped diverticula and a third sac-diverticulum above the bulb, the latter being a big excretory papilla, all these diverticula with intense yellow colour. Stomach and radial canals also yellow, but less intense than diverticula.

16S data: The partial 16S gene sequence obtained was used to search for similar sequences in GenBank using the blastn function. The results were mostly thecate hydroids, but only with a maximal identity of 83%.

Distribution: Florida. Type locality: USA, Florida, Dry Tortugas archipelago.

Remarks: The observed medusae were smaller (2.5-4 mm) than given in Mayer (1910, 8 mm), but Vanhöffen reported also animals of this size and two of our specimens were actually the result of a fragmentation and regeneration. Mayer (1910) had seen only immature animals. One of ours had bulges on the radial canals that we interpreted as the beginning of the gonad formation (Fig. 36A-D).

The small size and vigorous swimming style made it difficult to get good photographs in the sea and the resulting images are unfortunately not so suitable for seeing more details of the bell margin in the living animals. However, the unique, yellow, lateral appendages of the marginal bulbs are unmistakable and the species is unambiguously identifiable. According to Mayer (1910) the appendages contain symbiotic algae (zooxanthellae). Although Mayer (1910) observed large swarms of this medusa, it is a very rare species. To our knowledge, it was only recorded after its first description by Vanhöffen (1913a), this from near the type locality.

Neither searches in GenBank nor sequence comparisons with a number of Leptothecata gave any hint for relationships with other families (results not shown).

Family Aequoreidae Eschscholtz, 1829

Genus *Aequorea* Péron & Lesueur, 1810

Aequorea Péron & Lesueur, 1810: 334; type species *Aequorea forskalea* Péron & Lesueur, 1810 by subsequent designation by Mayer (1910).

Mesonema Eschscholtz, 1829: 112.

Stomobrachiota Brandt, 1835: 220; type species *Stomobrachiota lenticularis* Brandt, 1835 by monotypy.

Stomobrachium Brandt, 1837: 189.

Mesonema (*Zygodactyla*) Brandt, 1838: 360; type species *Mesonema* (*Zygodactyla*) *coerulescens* Brandt, 1838 by monotypy.

Crematostoma A. Agassiz, 1862: 360.

Rhegmatodes A. Agassiz, 1862: 361.

Aequorea (*Aequoranna*) Haeckel, 1879: 219; type species *Aequorea discus* Haeckel, 1879 by monotypy.

Aequorea (*Aequorella*) Haeckel, 1879: 219.

Aequorea (*Aequoroma*) Haeckel, 1879: 220.

Aequorea (*Aequorissa*) Haeckel, 1879: 221; type species *Aequorea albida* Agassiz, 1862 by monotypy.

Rhegmatodes (*Regmatella*) Haeckel, 1879: 222.

Rhegmatodes (*Regmatissa*) Haeckel, 1879: 223.

Staurobrachium Haeckel, 1879: 224: type species *Aequorea stauroglypha* Péron & Lesueur, 1810 by monotypy.

Mesonema (*Mesonemanna*) Haeckel, 1879: 226.

Mesonema (*Mesonemella*) Haeckel, 1879: 226.

Mesonema (*Mesonemissa*) Haeckel, 1879: 226.

Diagnosis: Medusa manubrium very wide, circular; no gastric peduncle, but often with jelly cone within stomach; subumbrella without radial rows of gelatinous papillae. With numerous, unbranched radial canals, new radial canals develop centrifugally from stomach base. Gonads on radial canals, separated from manubrium.

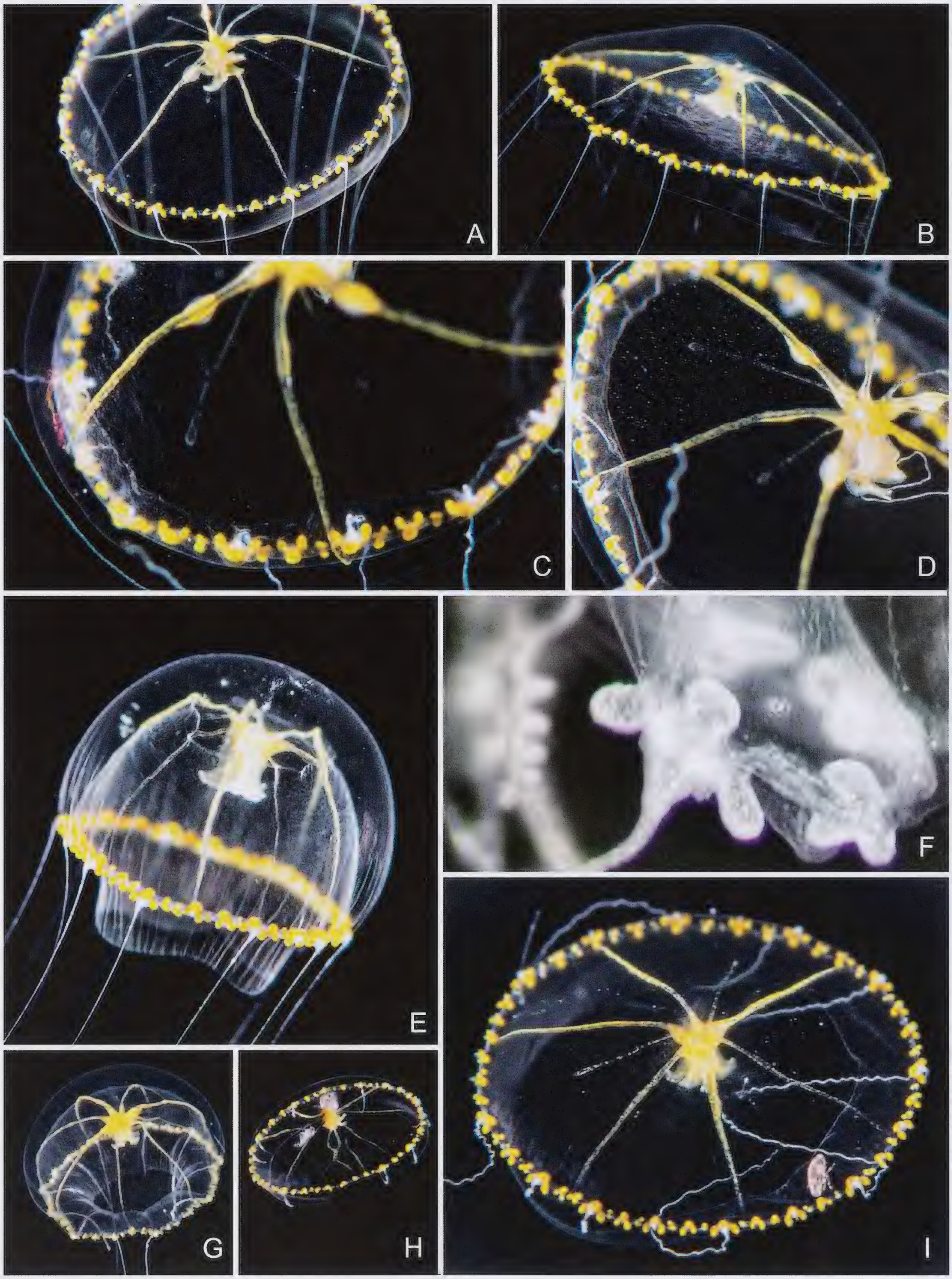


Fig. 36. *Wuvula ochracea*. (A-D) Animal observed 04-JUN-2019, ca. 2.5 mm, different views of the same animal, note beginning gonad development on radial canals. (E) BFLA4392, size 4 mm. (F) BFLA4372, preserved sample, view from adaxial side on a bulb with its appendages. (G) BFLA4470, size 3.5 mm. (H) BFLA4361, size 3.5 mm. (I) Animal observed 16-MAR-2020, not collected, size 4 mm.

Marginal tentacles hollow; usually with excretory pores or papillae on adaxial side of base; no marginal or lateral cirri; statocysts closed; no ocelli.
Hydroid where known of 'campanulinid' type, small usually lacking species-specific characters (see Bouillon *et al.*, 2006).

Remarks: *Aequorea* is a difficult genus as can be suspected from the complex synonymy given above. A comprehensive revision of its species is needed (Purcell, 2018). Kramp (1961) plainly expressed "The species are more or less doubtful." Russell (1953) had similar thoughts. However, both experts contributed much in consolidating and establishing a workable species level taxonomy which is still in use today.
Dawson (2004) and Zheng *et al.* (2009, 2014) have begun to study species level systematics using DNA sequences, but we are still missing sequence data for many populations and species and their correlation with morphotypes.
Here, we separated the species first using their 16S data and then searched for suitable names that matched their morphology. A few photographs of fully grown medusae that were not sampled could afterwards also be attributed to nominal species. It seems, however, that the sequence data are not really congruent with described nominal species. While the species level diversity is higher than expected, it is also surprising that some have a much wider distribution than thought before [see also Pruski & Miglietta (2019) for *A. australis* and its occurrence in the Gulf of Mexico].
Some additional species were examined for this study to allow a better comparison and species delimitation. This material is listed above in the section Material and Methods.

Aequorea neocyanea new name

Fig. 38A-I

Zygodactyla cyanea L. Agassiz, 1862: 361. [not *Aequorea cyanea* de Blainville, 1834]
Zygodactyla cyanea. – Agassiz, 1865: 107, fig. 159. – Haeckel, 1879: 227. – Mayer, 1900: 60, pl. 11 fig. 23 & 23a, pl. 15 figs 33-34. – Mayer, 1904: 17, pl. 3 figs 16-17.
in part *Aequorea forskalea*. – Mayer, 1910: 325, *Z. cyanea*as synonym.
? *Mesonema coelum-pensile*. – Vanhöffen, 1913a: 425, fig. C.
? *Aequorea macrodactyla*. – Nogueira *et al.*, 2016: fig. 1. [not *Aequorea macrodactyla* (Brandt, 1835)]

Material examined: BFLA3783; 1 specimen; 18-SEP-2018; size 50 mm, with gonads; part preserved in formalin and deposited as UF-013449, part in alcohol for DNA extraction; 16S sequence MW528633 – BFLA3822; 1 specimen; 25-OCT-2018; size 40 mm, with gonads; part preserved in formalin and deposited as UF-013427, part in alcohol for DNA extraction; 16S sequence MW528634. – BFLA3827; 1 specimen; 14-NOV-2018; size 50 mm, with gonads; part preserved in formalin and deposited as UF-013435, part in alcohol for DNA extraction; 16S sequence MW528635. – BFLA4043; 1 specimen; 01-APR-2019; size 50 mm, with gonads; part preserved in formalin and deposited as UF-013436, part in alcohol for DNA extraction; 16S sequence MW528636. – BFLA4082; 1 specimen; 07-MAY-2019; size 55 mm, with gonads; part preserved in formalin and deposited as UF-013787, part in alcohol for DNA extraction; 16S sequence MW528669. – BFLA4083; 1 specimen; 07-MAY-2019; size 42 mm, with gonads; part preserved in formalin and deposited as UF-013788, part in alcohol for DNA extraction; 16S sequence MW528670. – BFLA4085; 1 specimen; 07-MAY-2019; size 60 mm, with gonads; part preserved in formalin and deposited as UF-013789, part in alcohol for DNA extraction; 16S sequence MW528671. – BFLA4236; 1 specimen; 21-OCT-2019; size 30 mm, with gonads; part preserved in formalin and deposited as UF-013844, part in alcohol for DNA extraction; 16S sequence MW528689. – BFLA4304; 1 specimen; 15-JAN-2020; size 90 mm, with gonads; part preserved in formalin and deposited as UF-013881, no tissue sample. – 1 specimen photographed 08-FEB-2017, not collected; size 100 mm, with developed gonads. – 1 specimen photographed 06-JUN-2020, not collected; size 70 mm, with developed gonads.
The formalin samples are mostly strongly fragmented and damaged.

Taxonomy: In order to avoid a secondary homonymy with *Aequorea cyanea* de Blainville, 1834, we propose here the replacement name *Aequorea neocyanea* for *Zygodactyla cyanea* L. Agassiz, 1862. *Zygonema* Brandt, 1838 is a synonym of *Aequorea* Péron & Lesueur, 1810 (Ranson, 1949) and Agassiz' *Z. cyanea* must be transferred to *Aequorea*.

Observations: Typical *Aequorea* medusae, diameters of animals with well developed gonads 50 to 100 mm, sizes of animals without gonads (juveniles) up to 30-40 mm. Umbrella in fully grown animals relatively flat (Fig. 38A), about 1/4 of diameter, in younger ones more spherical. Stomach large, diameter 1/2 of bell diameter, with shallow jelly cone inside. Mouth rim with short fimbriae only (Fig. 38G), same number as radial canals, continued centrifugally as fine rib or streak on stomach and then as radial canal. Radial canals in mature animals 25 to 100, more commonly 60 to 80, lower number might also be due to regeneration from fragments. A few (2-4) incomplete radial canals growing centrifugally can be present, also irregularities like fusions or branching, but these likely of traumatic origin. Gonads along radial canals, spanning from almost the beginning to a short distance from circular canal (Fig. 38A-B), bilamellar, when fully developed large and hanging into subumbrella like a curtain, walls much folded or undulated (Fig. 38A). Fully formed

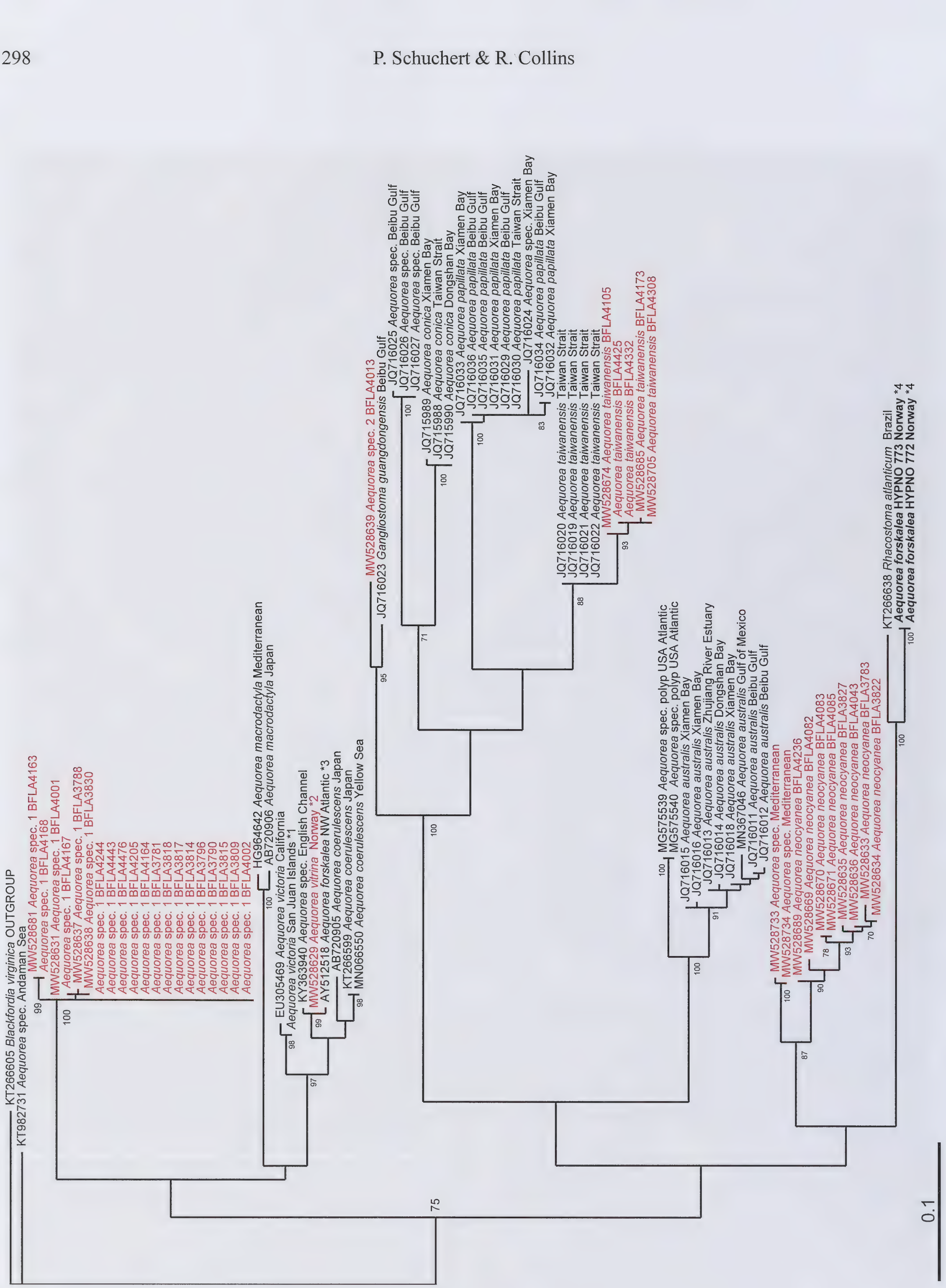

KT266605 Blackfordia virginica OUTGROUP
KT982731 Aequorea spec. Andaman Sea
MW528681 Aequorea spec. 1 BFLA4163
Aequorea spec. 1 BFLA4168
MW528631 Aequorea spec. 1 BFLA4001
Aequorea spec. 1 BFLA4167
MW528637 Aequorea spec. 1 BFLA3788
MW528638 Aequorea spec. 1 BFLA3830
Aequorea spec. 1 BFLA4244
Aequorea spec. 1 BFLA4443
Aequorea spec. 1 BFLA4476
Aequorea spec. 1 BFLA4205
Aequorea spec. 1 BFLA4164
Aequorea spec. 1 BFLA3781
Aequorea spec. 1 BFLA3818
Aequorea spec. 1 BFLA3817
Aequorea spec. 1 BFLA3814
Aequorea spec. 1 BFLA3796
Aequorea spec. 1 BFLA3790
Aequorea spec. 1 BFLA3815
Aequorea spec. 1 BFLA3809
Aequorea spec. 1 BFLA4002
HG964642 Aequorea macrodactyla Mediterranean
AB720906 Aequorea macrodactyla Japan
EU305469 Aequorea victoria California
Aequorea victoria San Juan Islands *1
KY363940 Aequorea spec. English Channel
MW528629 Aequorea vitrina Norway *2
AY512518 Aequorea forskalea NW Atlantic *3
AB720905 Aequorea coerulescens Japan
KT266599 Aequorea coerulescens Japan
MN066550 Aequorea coerulescens Yellow Sea
MW528639 Aequorea spec. 2 BFLA4013
JQ716025 Aequorea spec. Beibu Gulf
JQ716023 Gangliostoma guangdongensis Beibu Gulf
JQ716026 Aequorea spec. Beibu Gulf
JQ716027 Aequorea spec. Beibu Gulf
JQ715989 Aequorea conica Xiamen Bay
JQ715988 Aequorea conica Taiwan Strait
JQ715990 Aequorea conica Dongshan Bay
JQ716033 Aequorea papillata Xiamen Bay
JQ716036 Aequorea papillata Beibu Gulf
JQ716035 Aequorea papillata Beibu Gulf
JQ716031 Aequorea papillata Xiamen Bay
JQ716029 Aequorea papillata Beibu Gulf
JQ716030 Aequorea papillata Taiwan Strait
JQ716024 Aequorea spec. Xiamen Bay
JQ716034 Aequorea papillata Beibu Gulf
JQ716032 Aequorea papillata Xiamen Bay
JQ716020 Aequorea taiwanensis Taiwan Strait
JQ716019 Aequorea taiwanensis Taiwan Strait
JQ716021 Aequorea taiwanensis Taiwan Strait
JQ716022 Aequorea taiwanensis Taiwan Strait
MW528674 Aequorea taiwanensis BFLA4105
Aequorea taiwanensis BFLA4425
Aequorea taiwanensis BFLA4332
MW528685 Aequorea taiwanensis BFLA4173
MW528705 Aequorea taiwanensis BFLA4308
MG575539 Aequorea spec. polyp USA Atlantic
MG575540 Aequorea spec. polyp USA Atlantic
JQ716015 Aequorea australis Xiamen Bay
JQ716016 Aequorea australis Xiamen Bay
JQ716013 Aequorea australis Zhujiang River Estuary
JQ716014 Aequorea australis Dongshan Bay
JQ716018 Aequorea australis Xiamen Bay
MN367046 Aequorea australis Gulf of Mexico
JQ716011 Aequorea australis Beibu Gulf
JQ716012 Aequorea australis Beibu Gulf
MW528733 Aequorea spec. Mediterranean
MW528734 Aequorea spec. Mediterranean
MW528689 Aequorea neocyanea BFLA4236
MW528669 Aequorea neocyanea BFLA4083
MW528670 Aequorea neocyanea BFLA4085
MW528671 Aequorea neocyanea BFLA3827
MW528635 Aequorea neocyanea BFLA4043
MW528636 Aequorea neocyanea BFLA3783
MW528633 Aequorea neocyanea BFLA3822
MW528634 Aequorea neocyanea BFLA3822
KT266638 Rhacostoma atlanticum Brazil
Aequorea forskalea HYPNO 773 Norway *4
Aequorea forskalea HYPNO 772 Norway *4
0.1

Fig. 37. 16S maximum likelihood phylogenetic tree of the genus *Aequorea* and related genera obtained with PhyML (GTR+G+I model) using about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Red labels are new sequences from this study, for the taxa in bold either a voucher specimen or photos of it have been examined. Notes: *1) Unpublished, L. Leclère, pers. comm. *2) See Material & Methods. *3) Could be a misidentification. *4) Unpublished, A. Hosia & L. Martell, pers. comm., see Fig. 39A.

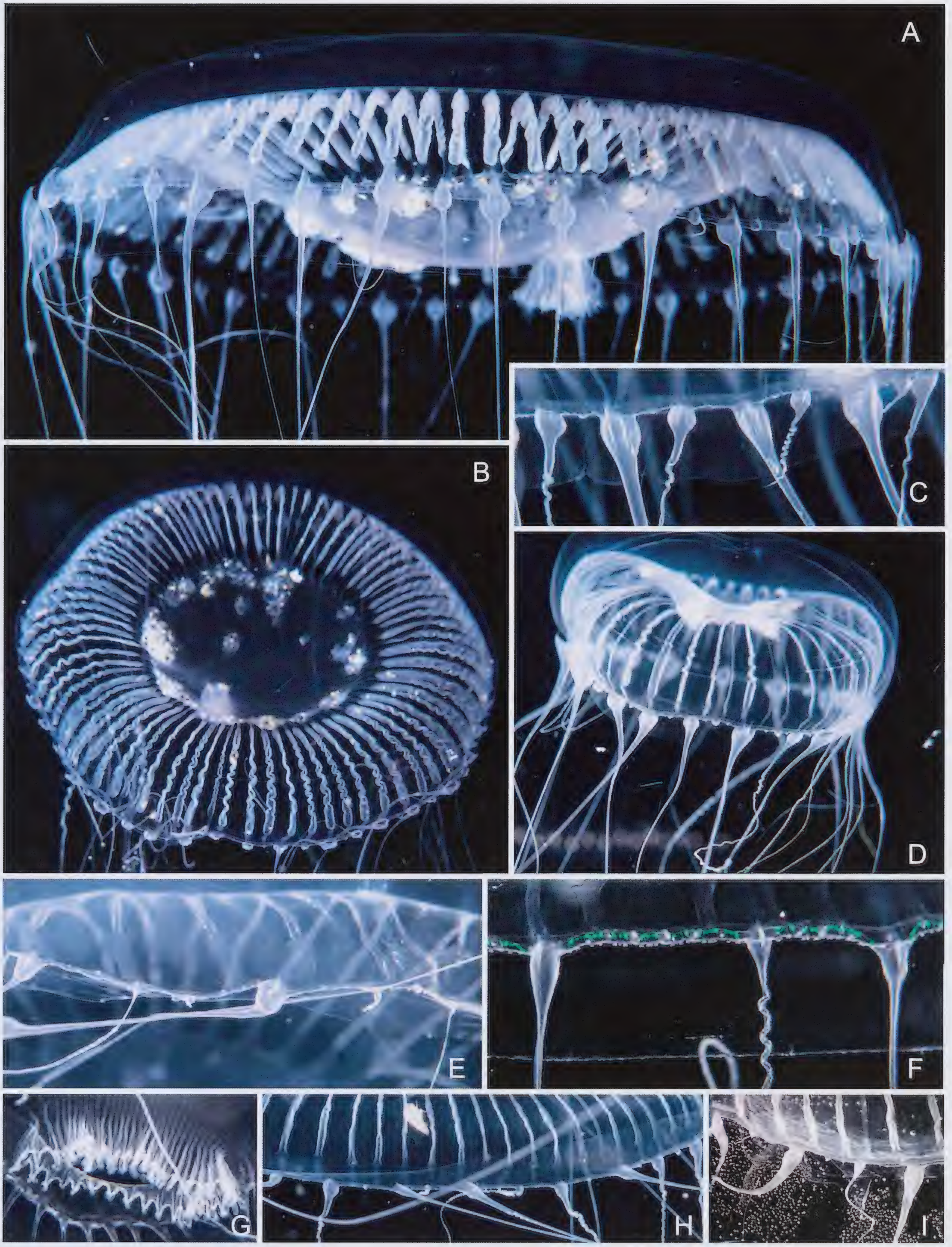


Fig. 38. *Aequorea neocyanea* new name. (A-C) BFLA4085, bell diameter 60 mm. (A) Oblique view from below. (B) Aboral view. (C) Bell margin with tentacles and their bulbs. (D) BFLA4083, bell diameter 42 mm, young animal with beginning gonad development. (E) BFLA4043, bell margin. (F) BFLA4236, bell margin, the green dots are not a pigment but likely due interference effects. (G) BFLA4236, mouth region with short fimbria. (H) BFLA3783, bell margin. (I) BFLA3783, tentacles after fixation in formalin.

tentacles 21 to 50, additionally some small ones or mere bulbs that will likely later also develop into tentacles. Observed ratios of radial canals to fully formed tentacles 1.0-3.0. Tentacles in life nearly always with a swollen base (Fig. 38C, E, F, H) degree of swelling is apparently modifiable and could depend on environment or physiological state as once the animal is preserved the swelling is much reduced (Fig. 38I). Regularly there is a faint abaxial keel, often emphasized or feigned by a whitish line on median of abaxial side (Fig. 38E, F, H) caused by an accumulation of nematocysts, this line only visible in living animals. In swollen bulbs abaxial side or keel often elongated into abaxial spur (Fig. 38A-D), in preserved material much less visible or absent. Excretory papillae absent, excretory pores could not be found reliably in the preserved material. Four or more statocysts (up to 14) between two tentacles or bulbs, 2-3 statoliths per statocyst. Colours: unpigmented, very well grown specimens with a pink hue.

16S data: The eight haplotypes had a range of divergences of 0.3-2.1 % (Table 1, intrapopulation variation). A maximum likelihood tree of the partial 16S sequence (Fig. 37) yielded a diverse but well-defined clade for this species. Its sister clade comprises two samples from the Mediterranean diverging in 3.7-5.2% of their aligned bases (see discussion below). No relationship to *A. forskalea* nor to *A. macrodactyla* is evident though.

Distribution: Florida, Bermuda, perhaps also Brazil and even Mediterranean (see below). Type locality: Atlantic Ocean, USA, Florida, Key West.

Remarks: We think that the present material most likely belongs to the same species identified by Mayer (1900, 1904) as *Zygodactyla cyanea,* although there are some differences. *Zygodactyla cyanea* was first described by L. Agassiz (1862) based on animals from Key West, Florida. His brief description was later expanded (A. Agassiz, 1865) and a figure of a fully-grown animal provided. Agassiz (1865) reported it in great numbers along the Florida Reef. Mayer (1900, 1904) then added more details using material from Florida and the Bahamas, notably also figures of the tentacle bulbs and of younger stages. As Mayer was a collaborator of A. Agassiz, his identification was certainly discussed with the latter. In his 1910 monograph, Mayer then synonymized *Z. cyanea* with *Aequorea forskalea* Péron & Lesueur, 1810 without further discussion.

Our material matches more *Z. cyanea* of Mayer (1900, 1904) and not *A. forskalea* for the following reasons:

1) Mayer found it as very common off the coast of Florida and in our study it was likewise a frequent medusa.
2) The type locality is in the same region and connected by the Gulf stream.
3) Mayer describes and depicts the tentacle bulbs with an abaxial spur, but incorrectly identified it as an exumbrellar excretory papilla (which is unknown in hydromedusae). This corresponds to the bulbs we found (Fig. 38), although this trait is not a unique diagnostic feature for the species as it occurs also in *Aequora* spec. 1 (see below) and others, e.g. *A. krampi* Bouillon, 1984. *Aequorea forskalea* in current understanding has evenly tapering, not much swollen tentacle bases (Fig. 39).
4) The mature animals examined genetically had diameters of 5 to 6 cm, a stomach width of 1/2 the bell diameter, and up to 100 radial canals, thus matching Agassiz' and Mayer's values.

There are also traits that do not match. Notably our maximum tentacle number was about 50 and the ratio of radial canals to tentacles usually in the region of 2. Mayer gives up to 100 tentacles and a ratio of 1. These traits are known to be very variable in this genus and should be used with caution to separate species. Moreover, we found that *Aequorea* medusae often get fragmented and then reconstituted themselves. This vegetative reproduction via fission could account for much of the variation seen in the *Aequorea* (see Stretch & King, 1980).

Contrary to Mayer (1910), we think that Agassiz' medusa should be kept distinct from *A. forskalea*. The 16S sequences of our material were different from

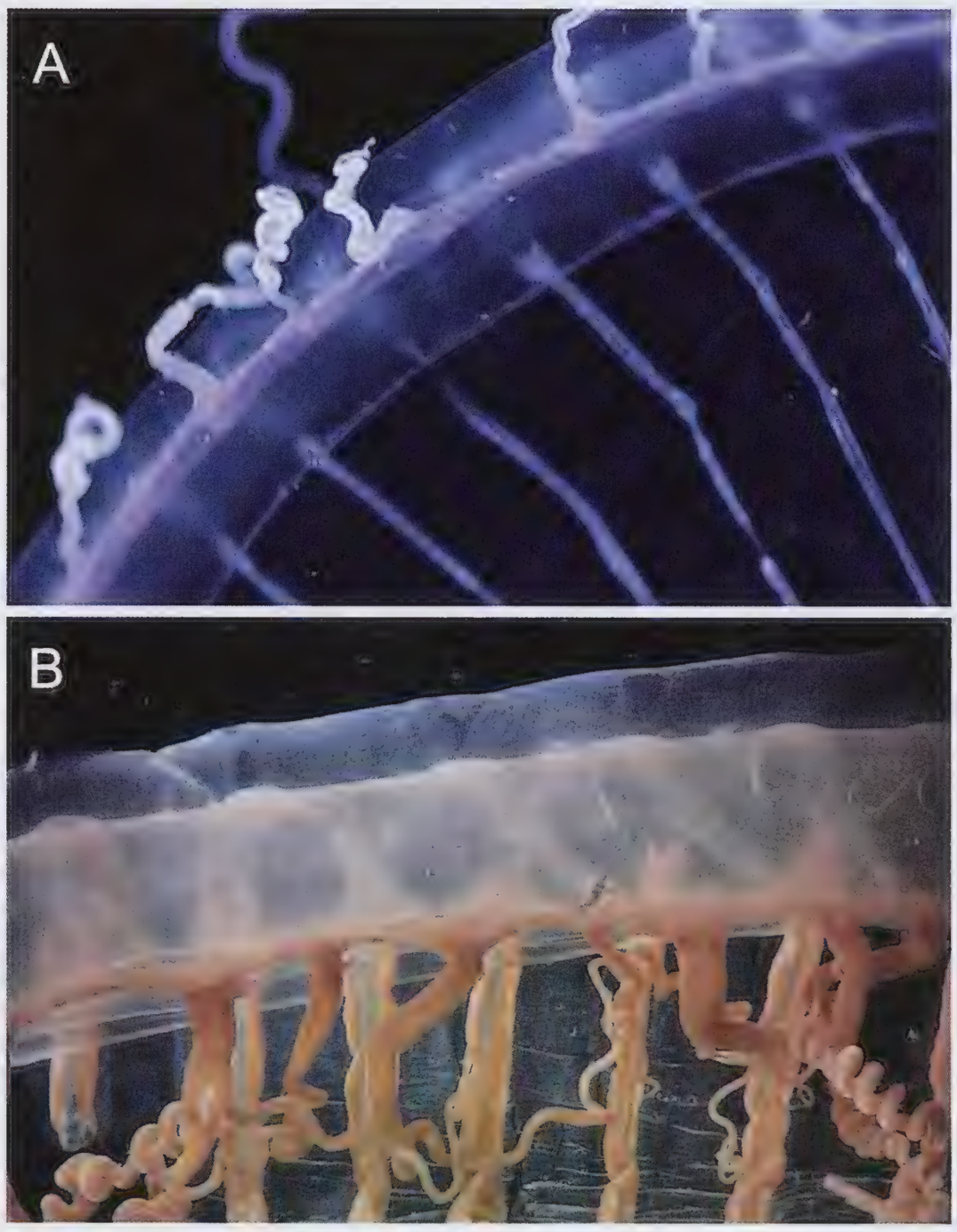


Fig. 39. *Aequorea forskalea.* (A) Living medusa from Norway, bell margin seen from oral side. Photo courtesy of Luis Martell, sample HYPNO 772. (B) Preserved sample from the Mediterranean, MHNG-INVE-0055261.

A. forskalea of the NE Atlantic (Fig. 37), the bell sizes were smaller than for typical *A. forskalea*, and tentacles bases are usually swollen and may have an abaxial keel and spur.

The name *Aequorea forskalea* was introduced by Péron & Lesueur, 1810 to replace the preoccupied name *Medusa aequorea* Forsskål, 1775 and they formally also restricted the type locality to the Mediterranean Sea. Forsskål (1775) provided a good illustration of his medusa which he had seen in the NE Atlantic or the Mediterranean and which we must assume to represent the type specimen. Forsskål's medusa was quite large with a diameter of 23 cm [in his Latin description he states "*Diameter spithamalis*", a spithame being an ancient Greek/Byzantine length unit corresponding to 0.231 m]. Our current scope of the species was outlined by Russell (1953) and Kramp (1959a) who give sizes of up to 175 mm and 60-80 radial canals. The bases of the tentacles are almost invariably given as evenly tapering and not swollen (Fig. 39, see also Kramp, 1959a: fig. 234b). This is clearly different to the ones observed here (Fig. 38) but some cautionary remarks are necessary. The degree of inflation of the tentacle base, the keel formation, and the abaxial spur seem to be variable and a partly transient feature. The swelling depends perhaps on the activity of the animal, the osmotic situation, or the digestive cycle. In preserved animals it is much less pronounced (Fig. 38I), but still apparently different from *A. forskalea*.

The status of the closely related Mediterranean *Aequorea* samples (Fig. 37, MW528733 and MW528734, see Material & Methods) is not clear. They were immature and 4 to 5 cm in size and their tentacle bases resembled the ones shown in Fig. 38E and not Fig. 39B. It could be that they also belong to the present species. The *A. forskalea* of the Mediterranean also differentiate into two morphotypes when examined alive (unpublished observations): one with slender, evenly tapering tentacles as shown in Fig. 39B and another with much swollen bases of the bulbs resembling the ones shown in Fig. 38A-B.

The Brazilian medusae identified as *A. macrodactyla* by Nogueira *et al*. (2016) do not match well the latter species (see Kramp, 1968; Schuchert, 2017a) but conform much better with the scope of *A. neocyanea* as documented here.

The status of the Mediterranean *Aequorea* morphotypes as well as many other populations should be examined using genetic techniques.

Aequorea spec. 1

Fig. 40A-K

Material examined: BFLA3781; 1 specimen; 18-SEP-2018; size 9 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3788; 1 specimen; 24-SEP-2018; no size data, no gonads; preserved in alcohol for DNA extraction; 16S sequence MW528637. – BFLA3790; 1 specimen; 24-SEP-2018; no size data, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631 – BFLA3796; 1 specimen; 13-OCT-2018; size 6 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3809; 1 specimen; 19-OCT-2018; size 10 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3814; 1 specimen; 20-OCT-2018; size 12 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631 – BFLA3815; 1 specimen; 20-OCT-2018; size 10 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3817; 1 specimen; 20-OCT-2018; size 12 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3818; 1 specimen; 24-OCT-2018; size 8 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA3830; 1 specimen; 15-NOV-2018; size 7 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence MW528638. – BFLA4001; 1 specimen; 20-NOV-2018; size 13 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence MW528631. – BFLA4002; 1 specimen; 20-NOV-2018; size 17 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA4163; 1 specimen; 06-AUG-2019; fragments 4 and 6 mm, gonads developing; part preserved in formalin and deposited as FU-013813, part preserved in alcohol for DNA extraction; 16S sequence MW528681. – BFLA4164; 1 specimen; 06-AUG-2019; size 8 mm, no gonads; part preserved in formalin and deposited as FU-013814, part preserved in alcohol for DNA extraction; 16S sequence MW528682. – BFLA4167; 1 specimen; 06-AUG-2019; size 6 mm, no gonads; part preserved in formalin and deposited as FU-013815, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528638. – BFLA4168; 1 specimen; 06-AUG-2019; size 6 mm, no gonads; part preserved in formalin and deposited as FU-013816, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528681. – BFLA4205; 1 specimen; 23-AUG-2019; size 4 mm, gonads developing; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA4244; 1 specimen; 11-NOV-2019; size 10 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631 – BFLA4443; 1 specimen; 07-JUN-2020; size 10 mm, no gonads; part preserved in formalin and deposited as FA-014058, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528631. – BFLA4464; 1 specimen; 13-JUN-2020; size 9 mm, no gonads; preserved in

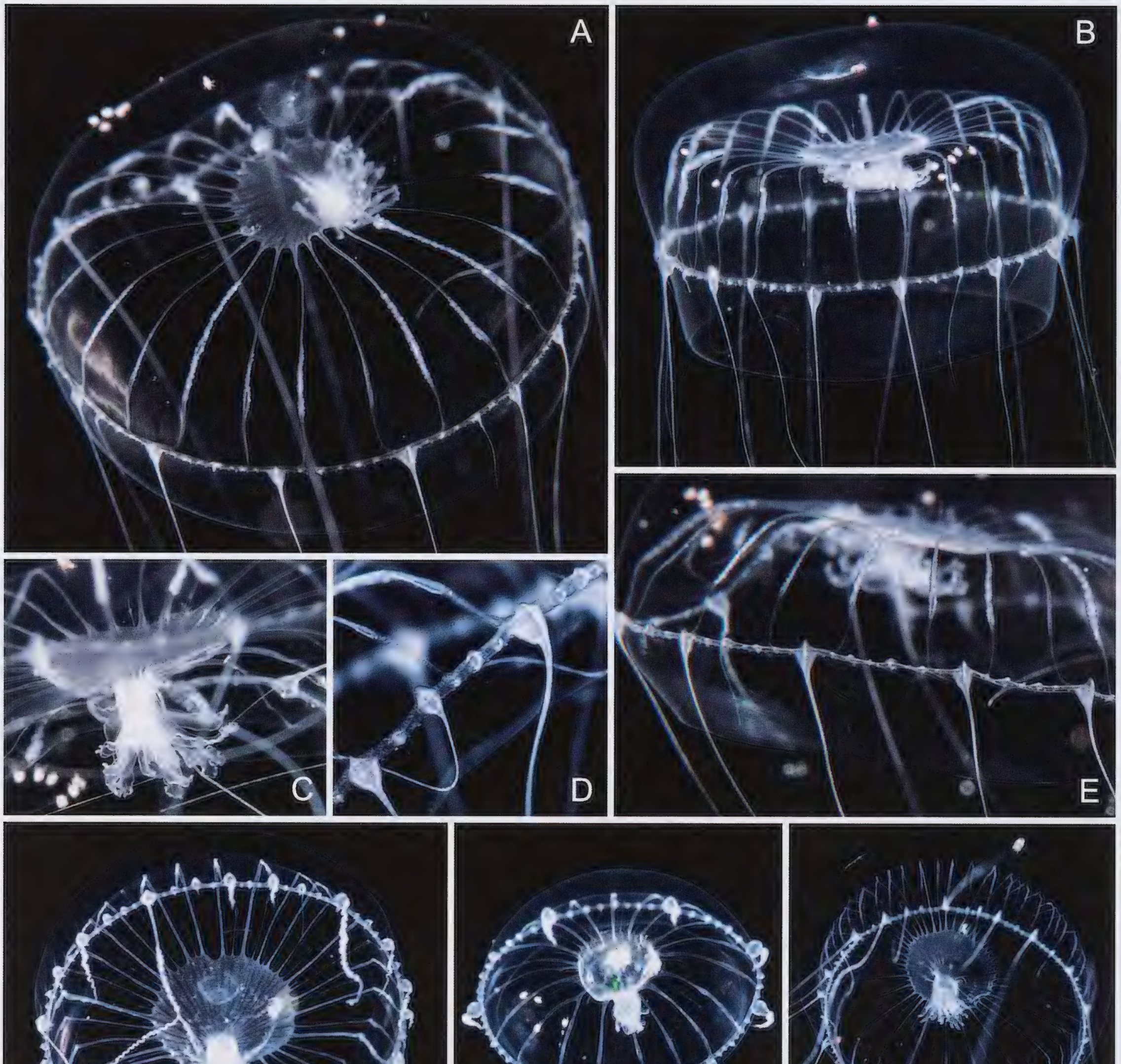


Fig. 40. *Aequorea* spec. 1. (A-B) BFLA4163, size > 10 mm. (C) BFLA4163, manubrium. (D) BFLA3814, close up of bell margin. (E) BFLA4163, close up of bell margin. (F) BFLA3814, size 12 mm. (G) BFLA3788, size not recorded. (H) BFLA4002, size 17 mm. (I) BFLA4002, bell margin from oral side, arrow points to excretory papilla. (J) BFLA3781, size 9 mm. (K) BFLA4476, size 5 mm, youngest observed stage with 6 complete radial canals, a large prey item is in the stomach.

alcohol for DNA extraction; 16S sequence identical MW528681. – BFLA4476; 1 specimen; 18-JUN-2020; size 5 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528631.

Observations: Small *Aequorea* medusae with bell diameters reaching 17 mm, only some with beginning gonad development (Fig. 40A-B), gonad development starts at about 9 mm size. Bell in smaller animals nearly hemispherical, larger ones more flattened. Stomach small, in the larger individual diameter ~1/4 to 4/5 of bell diameter. Mouth rim with many broad fimbriae (Fig. 40C). Radial canals thin, up to 46 seen, often also developing centrifugal canals. Gonads developing in some of the radial canals (Fig. 40A), but apparently not fully developed. Up to 25 fully developed tentacles, additionally 1-5 very small tentacles or small bulbs without tentacles. Ratio of radial canals to tentacles 1.3 to 1.8 in individuals with visible gonads, thus always more radial canals than tentacles. Tentacles in life with a distinct, short, conical basal bulb (Fig. 40A-B, D-E), with faint abaxial keel, emphasized or feigned by a whitish line on median of abaxial side (visible in life only), abaxial side of bulb usually continued onto exumbrella as a short abaxial spur (Fig. 40E). Conspicuous excretory papilla on adaxial side of tentacle bulbs (Fig. 40I), pointing into subumbrella. One to two statocysts between tentacles or small bulbs, statocysts with two statoliths.

16S data: The five haplotypes had a range of divergences of below 1.0 % (Table 1, intrapopulation variation). A maximum likelihood tree of the partial 16S sequence (Fig. 37) found no significant relationship to other congeners.

Remarks: This species was delimited by the 16S sequences. Were it not for the 16S data, we would have considered the specimens as juveniles or a smaller form of *A. neocyanea*, this notably for their resembling tentacle bulbs (comp. Figs 38E and 40E). However, the 16S sequence data (Fig. 37) separated them into two unrelated clades. The base pair differences between sequences of the two clades were >8.2%. The two sample sets cannot well be compared morphologically as they represent different developmental stages. None of the specimens of the present species had fully developed gonads. One difference we noted was the presence of a large excretory papilla in a majority of specimens of the present species.

We were initially tempted to identify this lineage as *Aequorea floridana* (L. Agassiz, 1862), a species also reported to be common along the cost of Florida and the Bahamas by Mayer (1900) [for descriptions see Mayer (1910) and Bigelow (1913, 1938)]. Mature *Aequorea floridana* have 16 to 24 radial canals and up to 80-100 tentacles (Mayer, 1910). Sixteen is the prevalent number of radial canals. Our specimens with gonads had 14 to 46 radial canals and consistently fewer tentacles than radial canals. It was mainly the low tentacle number which influenced our decision to reject an identity with *A. floridana*. The lack of fully developed animals and the lack of distinctive features made it advisable not to introduce a new species name. This is an unsatisfactory situation, but 16S data of fully-grown animals and also of typical *A. floridana* morphotypes are needed to solve the problem and to put a name on this lineage.

Aequorea taiwanensis Zheng *et al.*, 2009

Fig. 41A-G

Aequorea taiwanensis Zheng *et al.*, 2009: 110, fig. 1. – Zheng *et al.*, 2014: 63, 16S ML tree.

Material examined: BFLA4105; 1 specimen; 27-MAY-2019; size 27 mm, beginning gonad development; part preserved in formalin and deposited as UF-013793, part preserved in alcohol for DNA extraction; 16S sequence MW528674. – BFLA4173; 1 specimen; 09-AUG-2019; size 30 mm; part preserved in formalin and deposited as UF-013820, part preserved in alcohol for DNA extraction; 16S sequence MW528685. – BFLA4308; 1 specimen; 16-JAN-2020; size 31 mm, gonads visible; part preserved in formalin and deposited as UF-013846, part preserved in alcohol for DNA extraction; 16S sequence MW528705. – BFLA4332; 1 specimen; 31-JAN-2020; size 40 mm, gonads visible; part preserved in formalin and deposited as UF-013890, part preserved in alcohol for DNA extraction; 16S sequence identical MW528705. – BFLA4425; 1 specimen; 28-MAY-2020; size 50 mm, gonads visible; part preserved in formalin and deposited as UF-014051, part preserved in alcohol for DNA extraction; 16S sequence identical MW528705. – 1 specimen photographed 07-FEB-2020, not collected; size 30 mm.
The formalin samples are mostly strongly fragmented and damaged.

Observations: Subadult *Aequorea* medusae with bell diameters 30 to 50 mm, gonad development starts at about 30 mm size. Bell relatively high, apical jelly about 1/2 of bell height. Stomach wide, 7/10 of bell diameter. Mouth rim with numerous, long, thin fimbriae (Fig. 41B). Radial canals thin, 100 to 240, often also with 15 to 100 developing centrifugal canals. 14 to 25 fully developed tentacles, between pairs of tentacles 3-5 small bulbs without tentacles. Ratio of radial canals to tentacles 7.5 to 10, thus always many more radial canals than tentacles. Tentacles in life either with a distinct conical basal bulb with a slight depression of upper side (Fig. 41D) or widened laterally to give a T-shape (Fig. 41C, G). Abaxial spurs absent. Small, abaxial excretory papillae can be present, only seen in preserved material. Tentacle bases in preserved material usually also with lateral expansions (Fig. 41F), but some simply

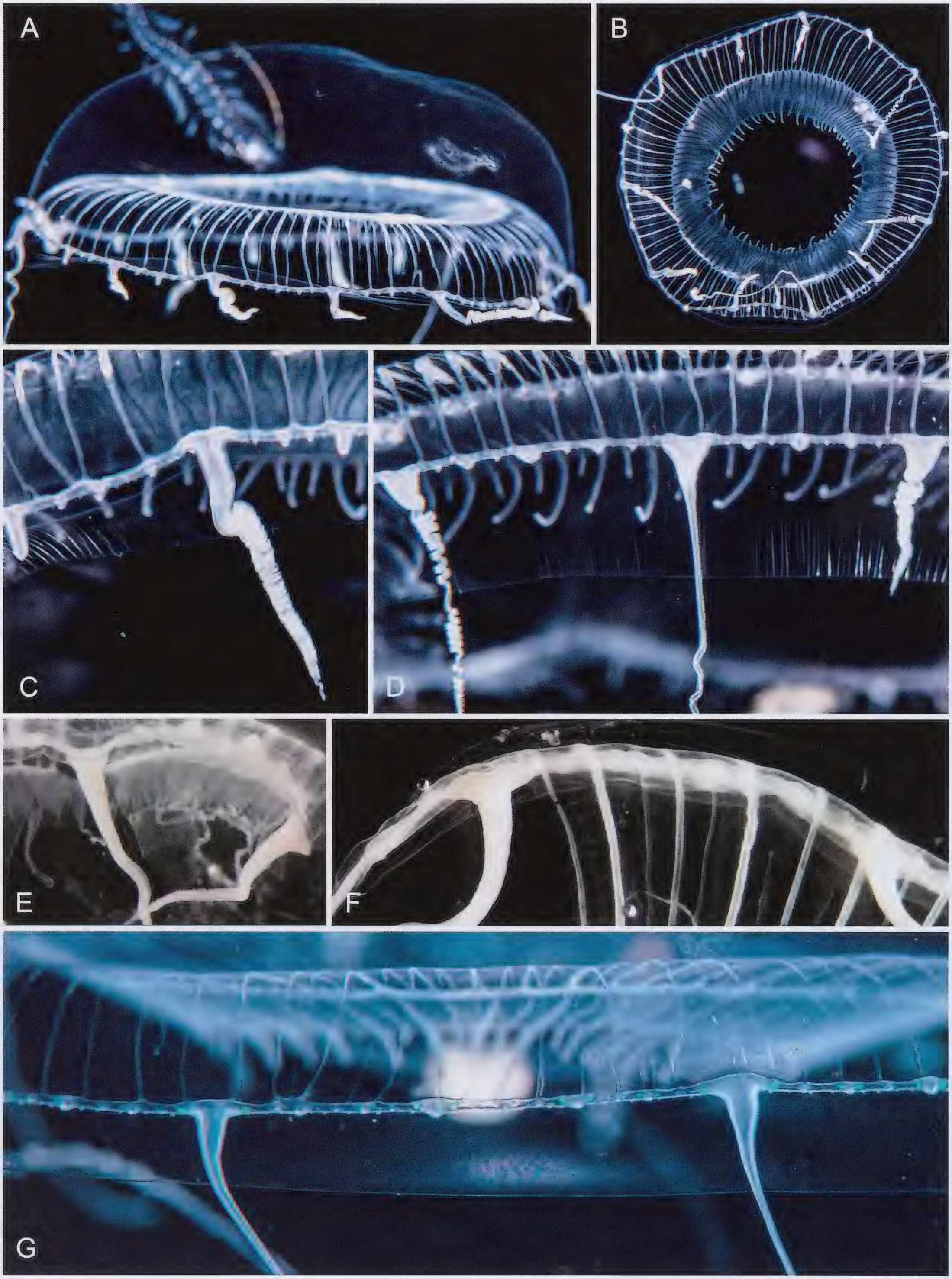


Fig. 41. *Aequorea taiwanensis*. (A-B) BFLA4308, size 31 mm. (C) BFLA4308, bell margin. (D) BFLA4332, bell margin. (E) BFLA4308, bell margin after preservation. (F) BFLA4332, bell margin after preservation. (G) Bell margin of animal photographed 07-FEB-2020, size 30 mm; the green dots flanking the bulbs are likely due to interference effects and not a pigment.

conical (Fig. 41E). Statocysts about as numerous as radial canals but not in phase with them, two statoliths per statocyst.

16S data: The three haplotypes had a range of base pair divergences of 0.2 to 0.5 % (Table 1). The maximum likelihood tree of the partial 16S sequences (Fig. 37) identified them as very closely related to *A. taiwanensis* (p-distances 0.2-0.64%).

Distribution: Taiwan strait, Florida (this study). Type locality: Taiwan Strait.

Remarks: This material resembles very much *Aequorea pensilis* (Haeckel, 1879), only the lateral expansions of the bulbs are shorter and sometimes absent in preserved material, and small excretory papillae can be present. Our identification of the present material as *A. taiwanensis* was based on the strong similarity of the 16S sequences (Table 1). The haplotype divergences to the published sequences from Taiwan Strait were only 0.2 to 0.64%, while within the Florida population we found a maximal value of 0.5%, thus intra- and interpopulation divergences are in the same range. In the ML tree (Fig. 37) the distance of the two population appears higher than the values obtained by pairwise comparisons. This is due to the fact that another substitution model was used for the distance calculation and more importantly, the sequences from the Taiwan Strait specimens were 112 bases shorter at the 3' end, leading to a bias in the ML analysis. While the similarity of our sequences with *A. taiwanensis* almost certainly implies that our material is conspecific, it must be noted that so far no *Aequorea pensilis* 16S sequences are available. It might turn out that *A. taiwanensis* is in fact a synonym of *Aequorea pensilis*. *Aequorea taiwanensis,* according to the description in Zehng *et al.* (2009), resembles *A. pensilis* but lacks the diagnostic long lateral expansions of the tentacle base and it has excretory papillae (comp. Browne, 1905; Maas, 1905; Kramp, 1968: Fig. 268). In our material, the lateral expansions were present, but also not as wide as usually shown for *A. pensilis*. Our material is thus intermediate between *A. pensilis* and *A. taiwanensis*. The specimens of Zheng *et al.* (2009) measured only 25 mm, were thus likely younger than ours, which reached up to 50 mm diameter. Pacific *Aequorea pensilis* reach 100 mm in diameter (Kramp, 1968).

The Atlantic occurrence of a rare *Aequorea* medusa of the Western Pacific Ocean is surprising, but not unparalleled. Pruski & Miglietta (2019) recently found *Aequorea australis* in the Gulf of Mexico, a species formerly only known from the Indo-Pacific Ocean.

The presence of *A. taiwanensis* in the Atlantic Ocean must not be interpreted as a possible recent introduction. While we found three different haplotypes, the four samples from Taiwan Strait (Zheng *et al.*, 2014) represented only a single one. The higher haplotype diversity in the Altantic argues against a recent introduction from the Pacific. The species has likely a wide distribution.

Aequorea spec.2

Fig. 42

Material examined: BFLA4013; 1 specimen; 17-DEC-2018; preserved in alcohol for DNA extraction; 16S sequence MW528639.

Observations: Small, juvenile *Aequorea* medusa, 7 mm, no gonads. Stomach diameter 0.3 of bell diameter. About 30 broad radial canals. Tentacles not all visible, approximate range 18-30. Tentacle bulbs conical, not inflated, without keel or white abaxial line, without abaxial spurs.

16S data: The single sequence proved to be quite closely related to *Gangliostoma guangdongensis* Xu, 1983 (Fig. 37). The base pair differences in the pairwise aligned sequences were 3.6%.

Remarks: We found only one specimen of this lineage and it was too immature for being identified. Additionally, the animal was attempting to swallow a much lager ctenophore and was thus quite distorted. Its 16S sequence resembled the Chinese *Gangliostoma guangdongensis*. The genus *Gangliostoma* is distinguished from *Aequorea* by a papilla situated at the base of the stomach and between each pair of radial canals. This feature is not well documented and it is unclear what it is. No such papillae could be seen in the present specimen.

Fig. 42. *Aequorea* spec. 2. (A-B) BFLA4313, size 7 mm, oral view.

Genus *Zygocanna* Haeckel, 1879

Zygocanna Haeckel, 1879: 214, type species *Aequorea pleuronata* Péron & Lesueur, 1810 (Kramp, 1961).

Zygocannota Haeckel, 1879: 215, type species *Aequorea purpurea* Péron & Lesueur, 1810 by monotypy.

Zygocannula Haeckel, 1879: 216, type species *Aequorea undulosa* Péron & Lesueur, 1810 by designation of Mayer (1910: 339).

Diagnosis: Medusa manubrium wide, no gastric peduncle, subumbrella with or without radial rows of gelatinous papillae. With more than 16 radial canals, at least some branched, new radial canals develop centrifugally from stomach base. Tentacle bulbs usually with excretory papillae. Gonads on radial canals, separated from manubrium.

Zygocanna cf. *apapillatus* Xu, Huang & Guo, 2014

Fig. 43A-E

Zygocanna apapillatus Xu, Huang & Guo, 2014 in Xu *et al*., 2014: 912, fig. 344.

Examined material: BFLA4302; 1 specimen; 15-JAN-2020; preserved in alcohol for DNA extraction; 16S sequence MW528704.

Observations: Bell diameter 5 mm, in relaxed state wider than high, relatively flat, apical jelly about 1/3 of height thinning to bell margin. Manubrium relatively small, diameter >1/10 bell diameter, base irregularly star-shaped, wall with radiating vertical folds, these changing into the corners of 7 (9?) simple mouth lips (Fig. 43E). About 10 radial canals originate at manubrium base and some immediately branch once or twice so that about 16 radial canals reach the circular canal. In addition to the complete radial canals about 5 developing centrifugal canals that originate from manubrium or complete radial canal (Fig. 43E). 14 ovoid gonads in about middle of complete radial canals, each with up to 50 oocytes, colour bright yellow with a median colourless, transparent line. 61 long, thin tentacles arising from ovoid bulbs, bulbs bright yellow, few atentaculate, small bulbs also present. One statocyst between pairs of marginal bulbs.

16S Data: The single haplotype (MW528704) was used in a blastn search in GenBank and gave as best match with 94% identity *Cyclocanna producta* (KY570308) followed by several Mitrocomidae and Tiaropsidae with similar scores. A maximum likelihood phylogeny using a wide selection of leptomedusae also associated the sequence with the same families, but with insufficient bootstrap support (tree not shown).

Remarks: This medusa resembles closely *Zygocanna apapillatus* Xu, Huang & Guo, 2014 and it could be conspecific. We were nevertheless reluctant to attribute it to this species for reasons given below. *Zygocanna apapillatus* is a very rare medusa only known from two specimens collected off the coast of Vietnam. The first description is only available in Chinese (Xu *et al*., 2014), but an English translation and the figures are given in the WoRMS database (Schuchert, 2020; urn: lsid: marinespecies.org: taxname: 828546). Our specimen differs only minimally, having a smaller manubrium diameter, less radial canals, and a higher number of gonads. However, some incomplete, developing radial canals suggest that the final number of radial canals could be higher than observed in the only specimen we had. Based on morphology alone, traditional morphology-based systematics would have treated them as conspecific.

With its small stomach, *Zygocanna apapillatus* is an atypical member of the genus *Zygocanna* and the Aequoridae (comp. Kramp, 1968) and it likely belongs to another family. The comparison of the 16S sequence obtained from our specimen indicated a similarity and possible relationship with several Mitrocomidae and Tiaropsidae but without sufficient bootstrap support due to the poor resolving power of the 16S marker for relationships above the genus level. There was clearly no relationship with Aequoreidae (tree not shown). Mitrocomidae and Tiaropsidae are both characterized by open statocysts, an important taxonomic trait that distinguishes them from most other leptomedusae which have either closed or no statocysts (comp. Bouillon *et al*., 2006). Unfortunately, we were unable to determine if it had open statocysts (a microscopic examination of living tissue or of histologic sections is needed for this). Without this information a correct identification of the species is impossible. This also holds true for the original description of *Zygocanna apapillatus*. Because of this uncertainty we identified our specimen only as *Zygocanna* cf. *apapillatus*.

Family Malagazziidae Bouillon, 1984a

Genus *Octophialucium* Kramp, 1955

Octophialucium Kramp, 1955b: 256; type species *Octocanna medium* Kramp, 1955 (designation in Kramp, 1961).

Diagnosis: Medusa without gastric peduncle, manubrium with eight lips; usually eight radial canals, variable in some species from 6 to 11; gonads on radial canals, separated from manubrium; tentacle bulbs with adaxial excretory papillae; no permanent atentaculate marginal bulbs, only developing tentacular bulbs; with closed statocysts; no ocelli; no cirri.

Hydroid colony stolonal; hydrotheca pedicellate, with a conical operculum formed by numerous convergent segments that are not clearly demarcated from hydrothecal wall; hydranth with intertentacular web; gonothecae claviform, arising from stolons.

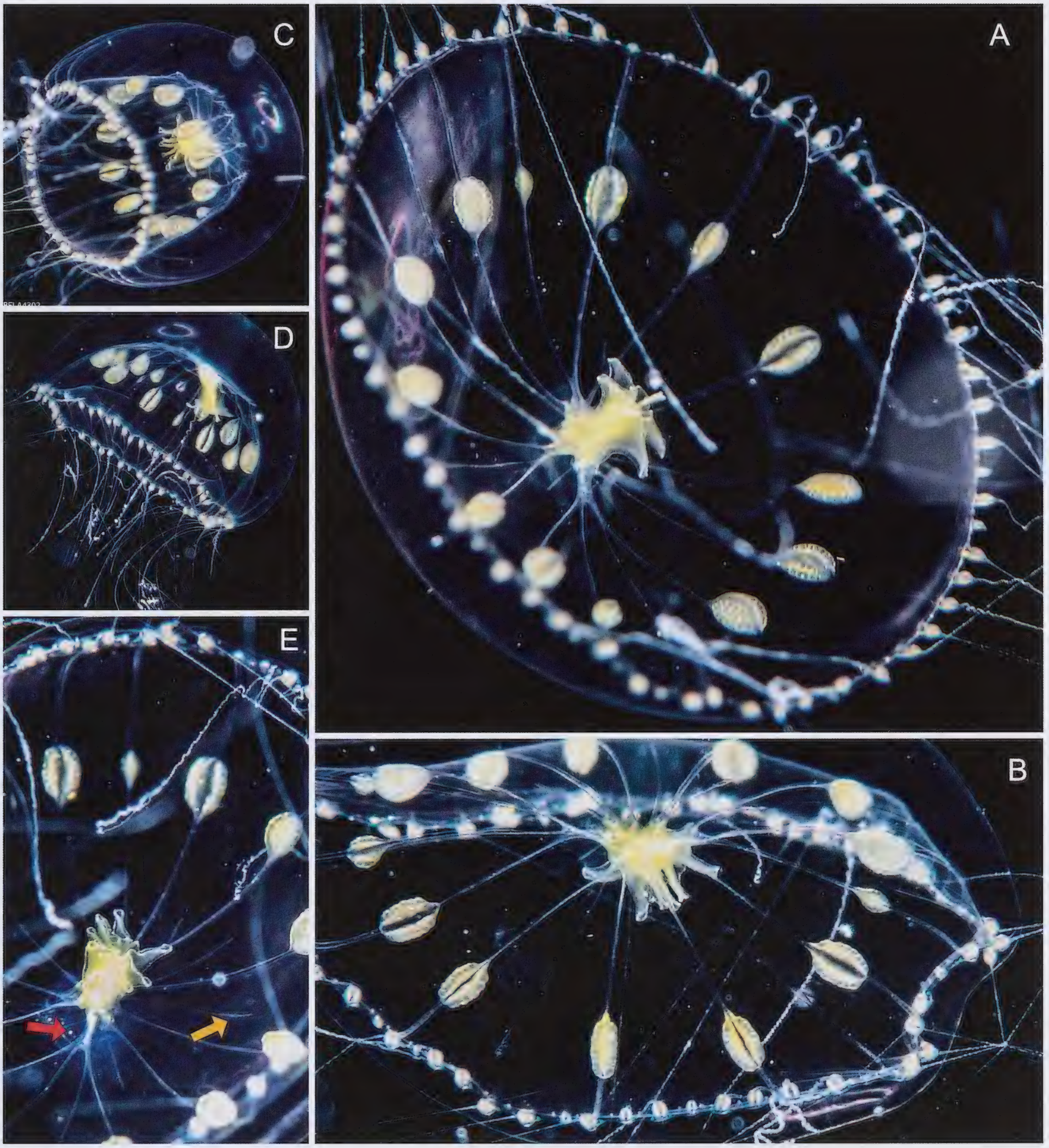


Fig. 43. *Zygocanna* cf. *apapillatus*, bell diameter 5 mm (A) Oral view. (B) Aboral view. (C-D) Lateral views. (E) Oral view, yellow arrow points to a developing radial canal, red arrow points to branching radial canal.

Octophialucium aphrodite (Bigelow, 1928)

Fig. 44A-F

Octocanna polynema. – Maas, 1906: 95, pl. 3 fig. 10. [not *Octocanna polynema* Haeckel, 1879 = indeterminate species]

Octocanna aphrodite Bigelow, 1928: 307, pl. 42 figs 1-2. – Stiasny, 1928: 212, fig. 2.

Octophialucium aphrodite. – Kramp, 1955b: 259, new combination. – Kramp, 1957: 35. – Kramp, 1961: 183. – Kramp, 1968: 89, fig. 239. – Bouillon, 1984b: 81, figs 25-26, life cycle, cnidome. – Wang *et al*., 2018: 108, fig. 3.

not *Octophialucium aphrodite*. – Van der Spoel & Bleeker, 1988: 170, fig. 27.

Examined material: BFLA3823; 1 specimen; 14-NOV-2018; size 24 mm; part preserved in formalin and deposited as UF-013428, part in alcohol for DNA extraction; 16S sequence MW528632. – BFLA3833; 1 specimen; 15-NOV-2018; size 10 mm; preserved in alcohol for DNA extraction; 16S sequence MW528630. – BFLA4130; 1 specimen; 11-JUN-2019; size 26 mm, 10 radial canals; part preserved in formalin and deposited as UF-013806, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528630. MHNG-INVE-0055283; 2 specimens, badly preserved; Indonesia, Moluccas, Bay of Ambon; collected 27.06.1890-02.09.1890; material described and figured in Maas (1906).

Observations on Florida specimens: Mature medusa diameter up to 26 mm, height about 10 mm, umbrella rather flat, apical jelly about half the height of the umbrella, lateral wall thin. Stomach large, tubular, base an eight-rayed star, mouth with eight long perradial lips, rim crenulated (Fig. 44A, E). Eight to 10 radial canals, tapering somewhat from manubrium to circular canal. Gonads along distal half of radial canals but not reaching to junction with circular canal, serpentine outline (Fig. 44A), in females with numerous small eggs. Tentacles about 90, tentacle-bulbs elongate conical, abruptly tapering into tentacle; most bulbs with a very large excretory papilla protruding into subumbrella from abaxial side above velum (Fig. 44B, arrow), excretory papilla in preserved animals much shrunken and rather small. Left and right of tentacle bulb base often a green spot (Fig. 44B), but which is not due to pigments. Very few incipient bulbs present. Tentacles thin, extensible to long size. One or two statocysts between tentacle pairs (Fig. 44B). Colour: circular canal with a light green tint, green spots flanking tentacle bulbs in living animals, otherwise colourless.

Immature medusa (BFLA3833, Fig. 44C) 10 mm in diameter; radial canals, circular canal, and bulbs green, incipient development of gonads, otherwise similar to adult.

16S Data: Searching GenBank for sequences similar to the obtained 16S sequences indicated a relationship to other leptomedusae, but gave no matches with more than 92% sequence identity. A maximum likelihood analysis of a wide selection of leptomedusae did not identify relationships with sufficient bootstrap support (results not shown). The two haplotypes differed in 0.8% of their base pairs.

Remarks: Morphologically, the adult specimen BFLA3823 matches very well the existing descriptions and figures (Bigelow, 1928; Kramp, 1968; Bouillon, 1984b) of *O. aphrodite*. Also the comparison material from the Moluccas agreed well [specimens described by Maas (1906) as *O. polynema*, later referred to *O. aphrodite* by Bigelow (1928)]. The 16S sequence divergence of 0.8 % for sample BFLA3823 and BFLA3833 was interpreted as intraspecific variation (see Table 1, and Schuchert *et al*., 2017). BFLA3833 is a subadult specimen and it was thus attributed to *Octophialucium aphrodite* mainly based on 16S sequence similarity.

It is somewhat surprising to find this Indo-Pacific medusa in the NW Atlantic Ocean, but it has already been recorded in the Gulf of Mexico by Canudas Gonzàlez (1979). However, the small size (11 mm), the low tentacle numbers (23-53), and the high number or radial canals (up to 15) given by Canudas Gonzàlez (1979) make this record somewhat doubtful. No illustration was provided. The animal depicted in Van der Spoel & Bleeker (1988) is unlikely *O. octophialucium* as it has only 24 tentacles. It is more likely *O. medium* Kramp, 1955b which has only 16 tentacles, but otherwise resembles *O. aphrodite* very much.

Octophialucium aphrodite resembles also closely *O. funerarium* (Quoy & Gaimard, 1827). The latter occurs in the NE Atlantic and the Mediterranean (Cornelius, 1995) and it appears more probable to be found in the western Atlantic than the Indo-Pacific *O. aphrodite*. Wang *et al*. (2018) have recently discussed some differences of the two species, mostly using the shape of the tentacular bulbs and the average number of statocysts between two fully developed tentacles (1 versus 2). However, there are more differences. Most importantly, the manubrium and the tentacle bulbs of *O. funerarium* are characteristically dark coloured by a black pigment (Quoy & Gaimard, 1827; Kramp & Damas, 1925; Russell, 1953; Cornelius, 1995). Moreover, the jelly is thicker and lentil-shaped, the subumbrella very shallow, the diameter is usually larger (up to 50 mm), and rudimentary bulbs are frequent (rare in *O. aphrodite*).

Bouillon (1984b) remarked that some published illustrations of *O. aphrodite* are based on altered specimens and he provided an excellent figure.

Based on the references given in the synonymy above, the following updated consensus diagnosis for *O. aphrodite* can thus be provided:

Medusa 15-40 mm in diameter when mature, bell flatter than hemisphere, apical jelly about half the height of the

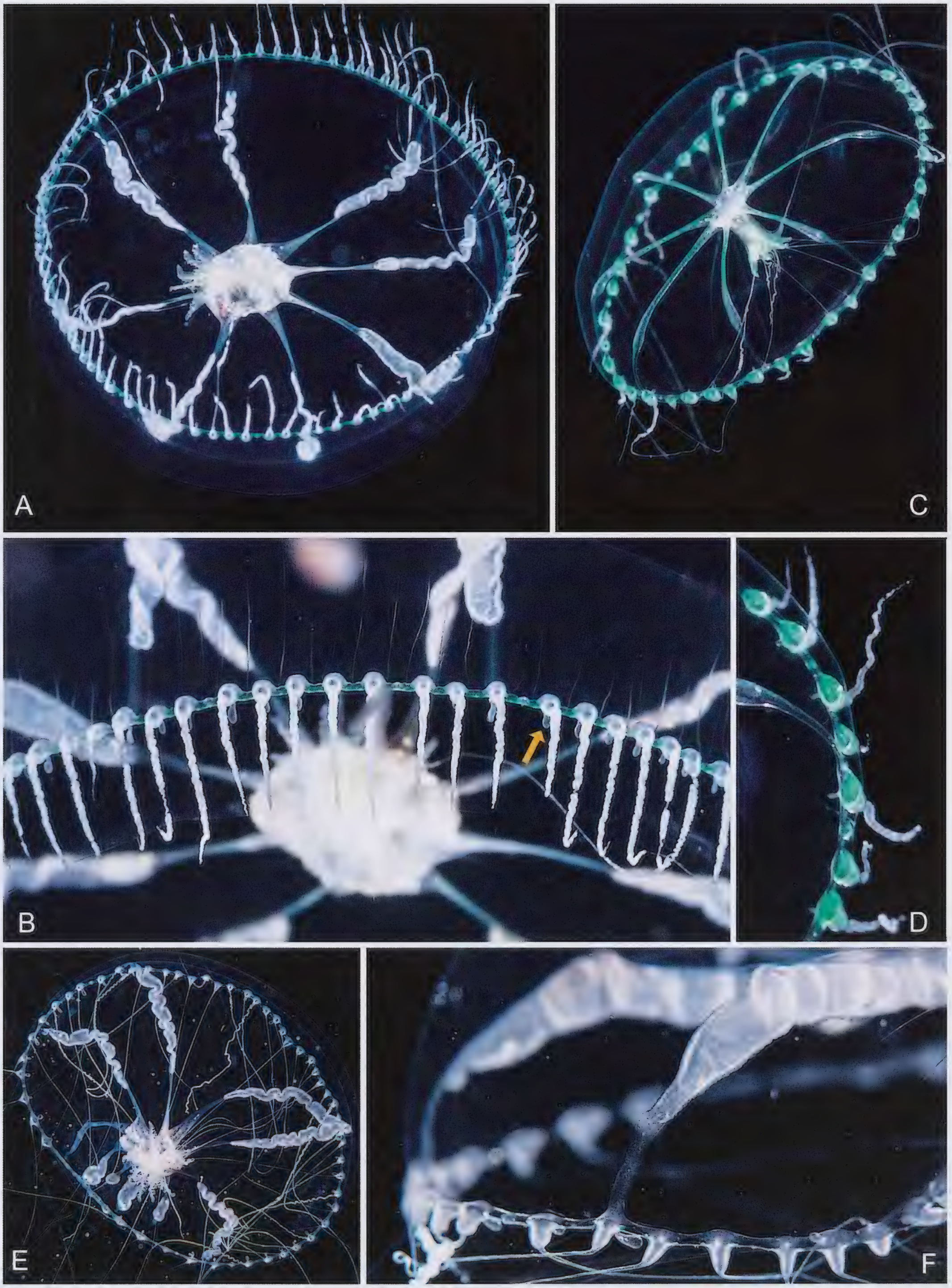


Fig. 44. *Octophialucium aphrodite*, living animals from Florida. (A) Oral view of whole animal BFLA3823, diameter 24 mm. (B) Close up of the bell margin of same animal as shown in A, bell opening facing down. Note the large excretory papillae (arrow) and the green dots flanking the marginal bulbs visible only in life. (C) BFLA3833, oblique aboral, bell diameter 10 mm. (D) Bell margin of medusa shown in C, seen from aboral side. (E) BFLA4130, bell diameter 26 mm, oblique view from oral side. (F) Bell margin of medusa shown in E.

bell, lateral wall thin. Manubrium large, tubular, base an eight-rayed star, mouth with eight perradial lips. Eight radial canals, rarely 7, 9, or 10. Gonads spindle-shaped, along distal 1/5 to 1/2 of radial canals, not reaching to junction with circular canal. 80-120 tentacles and as many bulbs, bulbs distinctly separated from tentacles, only few small bulbs without tentacles present. Excretory papillae tubular, large, in life reaching the same length as the bulbs. One or two statocysts between tentacle pairs, statocysts with two concretions. Colours: colourless or greenish circular canal, without black pigment in manubrium and bulbs.

Hydroid colony stolonal; hydrotheca pedicellate, with a conical operculum formed by numerous convergent segments that are not clearly demarcated from hydrothecal wall; hydranth with intertentacular web; gonothecae claviform, arising from stolons.

Distribution: In the Pacific Ocean known from Indonesia, Philippines, Papua New Guinea, and the South China Sea (Kramp, 1968; Bouillon, 1984b; Wang *et al*., 2018); in the Indian Ocean from the Mozambique Channel (Kramp, 1957); in the Atlantic Ocean perhaps in the Gulf of Mexico (Canudas Gonzàlez, 1979) and off Florida (this study). Type locality: Sulu Sea.

***Octophialucium irregularis* n.spec.**

Fig. 45A-G

Holotype: BFLA4290; observed and collected 19-DEC-2019; size 12 mm, with incipient gonads; part preserved in formalin and deposited as UF-013843, part preserved in alcohol for DNA extraction (MHNG-INVE-0137379); 16S sequence MW528701.

Other material: BFLA3829; 1 specimen; 15-NOV-2018; size 4 mm, juvenile; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA3838; 1 specimen; 19-NOV-2018; size 7 mm, without gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4131; 1 specimen; 11-JUN-2019; size 12 mm, without gonads; part preserved in formalin and deposited as UF-013807, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4259; 1 specimen; 30-NOV-2019; size 8 mm, incipient gonads; part preserved in formalin and deposited as UF-013838, much damaged, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4311; 1 specimen; 15-JAN-2020; size 5 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701. – BFLA4377; 1 specimen; 18-MAR-2020; size 6 mm, no gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528701.

Description: Bell diameter 8-12 mm for animals with gonads, bell rather shallow, apical jelly about half of height and subumbrella relatively shallow, soft walls and rim deformed easily. Velum narrow. Manubrium cross-section like a multi-rayed star (Fig. 45A-C, G), as many rays as radial canals, multi-rayed outline present from base to mouth, diameter narrowing towards mouth, mouth with about eight lips. Occasionally a secondary manubrium may be present. Radial canals 7-9, originating from manubrium rays, initially broad and then tapering, sometimes also one incomplete centrifugal canal present that does not reach circular canal. Arrangement of radial canals irregular, some irregularly curved, branching once, sometimes coalescing again or fusing with other radial canals, general appearance very variable, irregular, and disordered (Fig. 45A, D, G, F). Gonads arise in middle region of complete radial canals, oblong, slightly pendant (Fig. 45C), fully developed state unknown. Circular canal thin, in larger animals with incomplete centripetal canals arising from non-perradial bulbs, reaching about to mid-subumbrella height (Fig. 45D). Tentacles 27 to 30, on ovoid marginal bulbs which taper rapidly into thin tentacles, these often neatly coiled when contracted (Fig. 45E); bulbs with adaxial excretory papilla pointing into subumbrella, size variable, sometimes relatively large (Fig. 45C). Between tentaculate bulbs 1 to 3 smaller bulbs with very short tentacle (Fig. 45E) or without tentacle. Between successive marginal bulbs 1 to 3 closed statocysts with 2 statoliths (Fig. 45D-E). Colours: orange gastrodermis of tentaculate marginal bulbs, gonads orange; manubrium in younger stages transparent green (Fig. 45G), later whitish, sometimes at base in interradial position orange (Fig. 45A) or a weak interradial, brown pigment band from base to mouth (Fig. 45C).

16S Data: The seven specimens gave all an identical 16S sequence. The single haplotype (MW528701) was used in a blastn search in GenBank and gave as best match with 93% identity an *Octophialucium indicum* from New Zealand (AY787897). The pairwise identities with the 16S of *O. aphrodite* were lower, about 88%. A maximum likelihood tree using a wide selection of leptomedusae did not yield any well supported relationship (tree not shown).

Remarks: There are currently 11 accepted species of *Octophialucium* (Schuchert, 2020). In terms of size and tentacle numbers, the new species resembles only *Octophialucium mollis* Bouillon, 1984b, a species known from the tropical Western Pacific Ocean. *Octophialucium mollis* is also the only *Octophialucium* species that has centripetal canals. *Octophialucium irregularis* differs from *O. mollis* in the following aspects: it lacks the interradial rows of black spots on the manubrium wall (although in some there is a faint brown band, see Fig. 45C), the centripetal canals are longer, and the radial canals are very irregular in appearance and number. The latter feature is the most characteristic trait of this species and its specific epithet

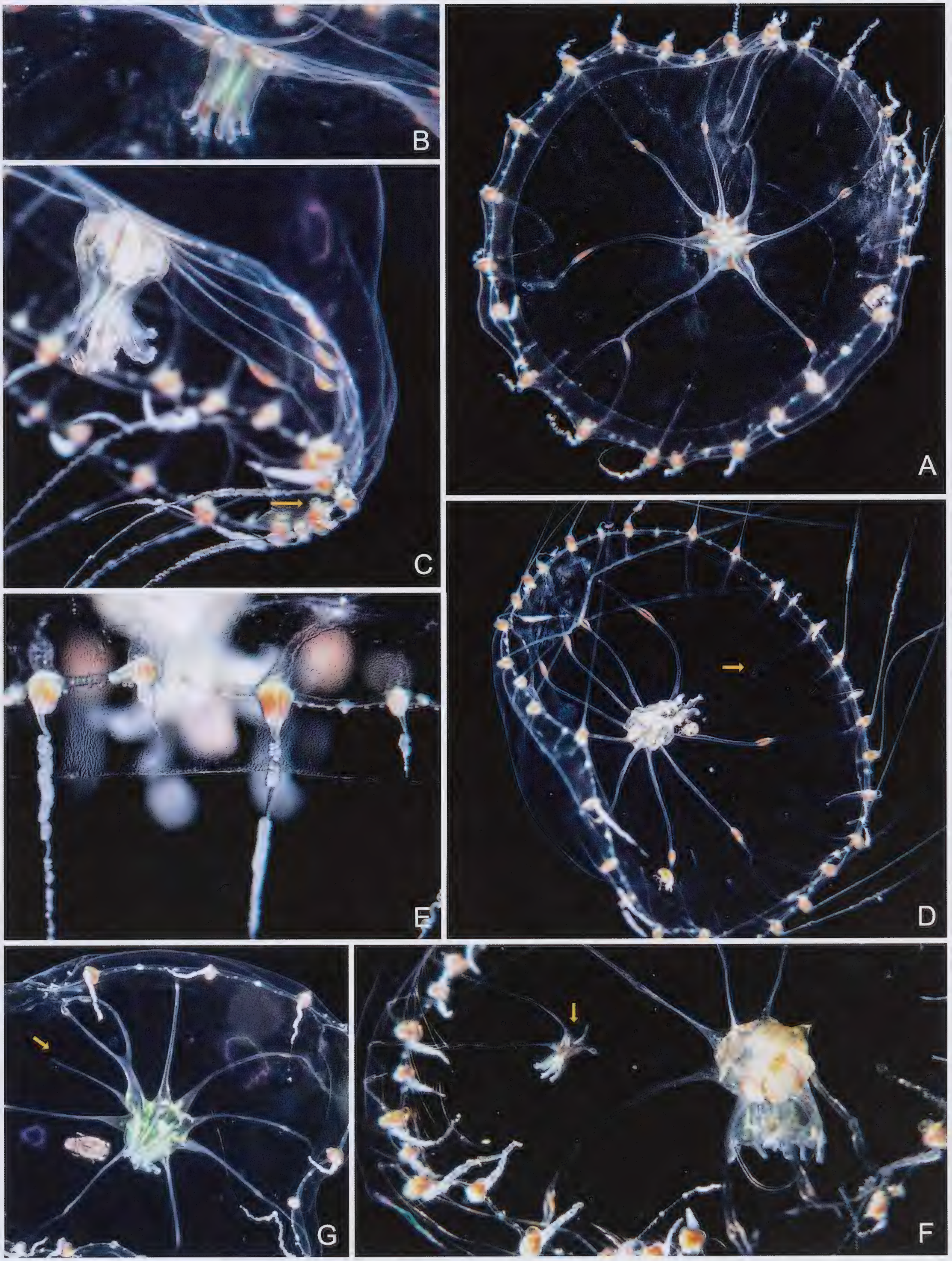


Fig. 45. *Octophialucium irregularis* n. spec. (A) Holotype, BFLA4290, aboral view, 12 mm diam. (B) BFLA4290, lateral view of manubrium. (C) BFLA4259, 8 mm, partial lateral view, arrow points to excretory papilla. (D) BFLA4259, oral view, arrow points to centripetal canal. (E) BFLA4259, bell margin, lateral view. (F) BFLA4131, 12 mm diameter, aboral view, arrow points to secondary manubrium. (G) BFLA3838, 7 mm oral view, arrow points to incomplete centrifugal canal.

irregularis is intended to reflect this. This irregular organisation is likely not only due to genetic factors, but – as irregularities of the bell margin suggest (Fig. 45A, G) – also due to repeated damage and subsequent regeneration.

Family Campanulariidae Johnston, 1836
Genus *Clytia* Lamouroux, 1812

Synonymy: See Calder (1991).

Diagnosis: Medusa with normal, curved umbrella. Manubrium short, with four short perradial lips. Velum present. Normally four radial canals, but some aberrant form may have more. Marginal tentacles >16, with hollow bulbs; without many permanent, small, conical atentaculate bulbs, no excretory papillae. With many statocysts (>16), usually as many or more as tentacles, no ocelli, no cirri. Gonads on radial canals, usually short, not in contact with manubrium.
Hydroid typical for family, colonial, stolonal or erect branched, monosiphonic or polysiphonic. Hydrothecae deep, campanulate, hydrothecal rim sinuous or deeply indented true hydrothecal diaphragm, gonotheca conical.

Remarks: Very few nominal species of *Clytia* medusae are unambiguously identifiable. Most morphological characters used to distinguish *Clytia* species fall in the range of variation that can be expected in a single species and having little or no taxonomic value (Lindner & Migotto, 2002; Bouillon *et al.*, 2006). Species identification requires usually knowledge of the entire life cycle. A recent extensive molecular phylogeny of the Campanulariidae (Cunha *et al.*, 2017) found even more taxonomic inconsistencies, and also provides an excellent framework for barcoding studies. The 16S data set of the latter study was used in a maximum likelihood phylogeny to search for relationships of the sequences obtained in this study. The tree is not shown here due to it size and the sparse results.

Clytia linearis (Thornely, 1900)
Fig. 46A-B

Obelia linearis Thornely, 1900: 453, pl. 44 fig. 6.
Clytia linearis. – Cornelius, 1982: 84, fig. 12. – Medel & Vervoort, 2000: 38, bibliography. – Peña Cantero & García Carrascosa, 2002: 149, fig. 28e-f, synonymy. – Lindner & Migotto, 2002: 541, figs 2-3, life cycle. – Schuchert, 2003: 160, fig. 20, synonymy. – Galea, 2007: 88, figs 20G-I, pl. 2J-K. – Galea, 2008: 20, fig. 4A-B. – Calder, 2013: 55, fig. 15f, record Florida, taxonomy.

Examined material: BFLA4077; 1 specimen; 16-APR-2019; size 3.5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528668.

Observations: Medusa 3.5 mm, bell when relaxed rather flat (Fig. 46A), height about 1/3 of diameter, jelly moderately thick. Manubrium small, four very short, simple perradial lips. Four radial canals, two of them (accidentally?) approximated and therefore not giving a perfectly tetraradial symmetry. Gonads male, very thick and long, sausage shaped, arising at short distance from manubrium and stretching to almost circular canal. 39 tentacles, each arising from a spherical basal bulb, thin and long. 1 to 2 atentaculate, smaller bulbs. At least as many or more statocysts as tentacles. Colour: all tissues with a green hue, transparent.

16S Data: The 16S sequence of our single sample was compared to the 16S dataset of Cunha *et al.* (2017). It was nested within the well supported *Clytia linearis* clade (tree not shown). Its sister clade is made up of the sequences AY789810 and AY346362 from Beaufort NC and the Mediterranean respectively (provenence acc. Govindarajan *et al.*, 2006). The sequence divergence from AY789810 is 2.5%.

Distribution: Circumglobal in shallow warm waters (Lindner & Migotto, 2002). Type locality: Papua New Guinea, New Britain, Blanche Bay (Thornely, 1900; hydroid).

Remarks: The identification of this medusa was based solely on its 16S sequence which was nested within a well supported *Clytia linearis* clade. The morphology matched rather well the description of *Clytia linearis* in Lindner & Migotto (2002) which was based on cultivated medusae. It only had slightly more tentacles and much larger gonads, both easily attributable to more optimal growth conditions. Notable were the rather flat umbrella and the small size.

Clytia spec. 1
Fig. 46C

Examined material: BFLA4240; 1 female; 11-NOV-2019; size 7 mm, with gonads; preserved in alcohol for DNA extraction; 16S sequence MW528690. – BFLA4283; 1 specimen; 06-DEC-2019; size 10 mm, with gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528690. – BFLA4342; 1 female; 29-FEB-2020; size 15 mm, with gonads; part preserved in formalin and deposited as UF-013895, part preserved in alcohol for DNA extraction; 16S sequence identical to MW528690.

Observations: Typical *Clytia* medusae, bell slightly shallower than hemisphere, diameters when mature 7 to 15 mm. Manubrium urn shaped, with four long perradial lips, margin undulated. Four radial canals. Gonads thick, ovoid to oblong, in middle of radial canal, about 1/5 of radial canal length. 18 to 22 tentacles arising from ovoid bulbs, 0 to 4 small atentaculate bulbs. Usually 2, sometimes 1 or 3, statocysts between pairs of bulbs, 2 statoliths per statocyst. Colour: radial canals in all three specimens with brilliant green colour.

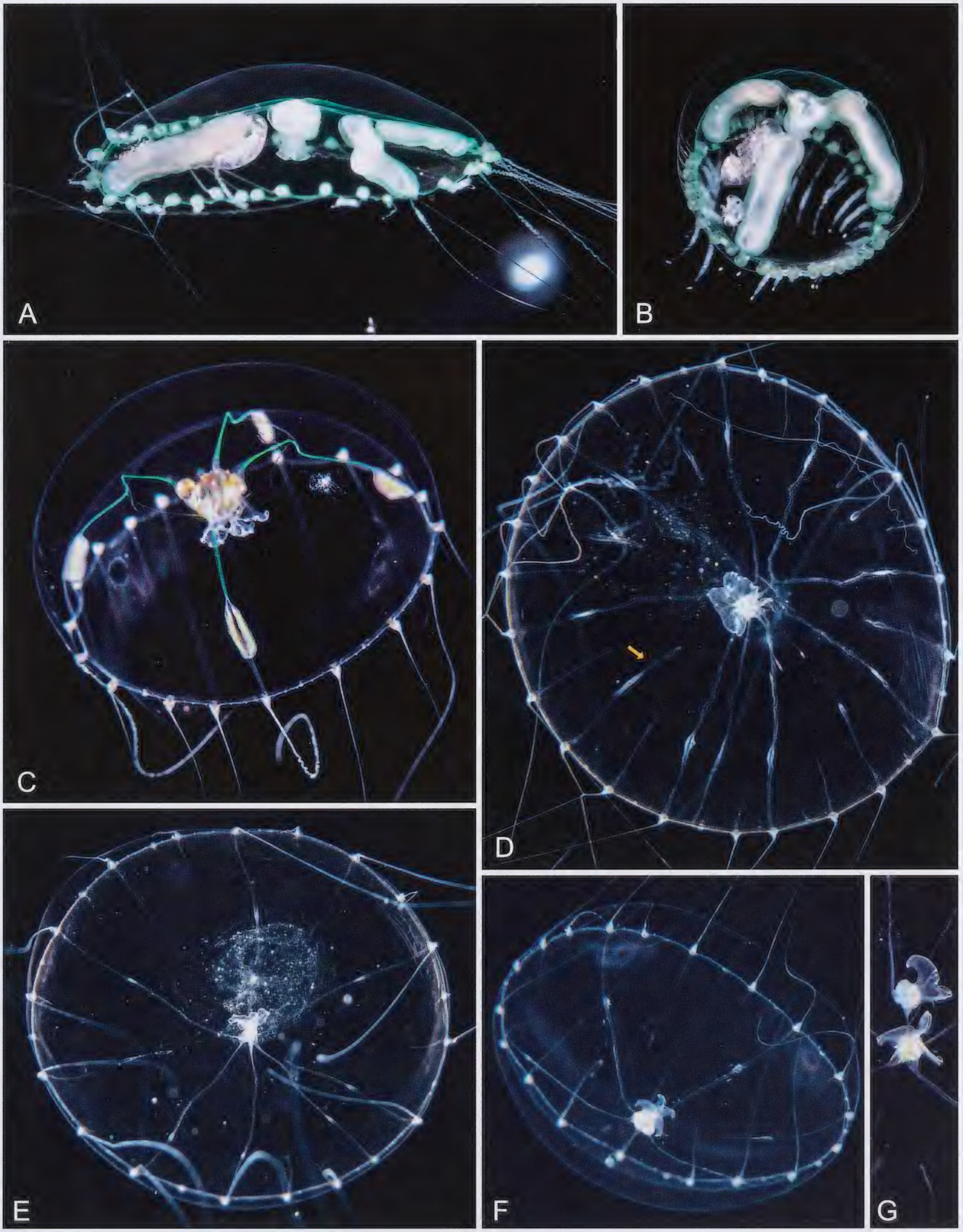


Fig. 46. *Clytia* ssp. (A-B) *Clytia linearis*, BFLA4077, bell dimeter 3.5 mm. (C) *Clytia* spec. 1, BFLA4283, bell diameter 10 mm. (D) ? *Clytia* spec. 2, BFLA4274, 3 mm; arrow points to incomplete centripetal canal. (E) ? *Clytia* spec. 2, BFLA4269, 4 mm. (F) ? *Clytia* spec. 2, BFLA4253, 3 mm, has 5 complete radial canals. (G) ? *Clytia* spec. 2, doubled manubrium of animal photographed 06-DEC-2019, 6 mm bell, not collected.

16S Data: The three samples gave all the same 16S sequence that did not show any sufficiently supported relationship to other *Clytia* medusae in the Campanulariidae 16S dataset of Cunha *et al.* (2017). A blastn search in GenBank gave *Clytia islandica* MF000548 as best match with 91% sequence identity.

Remarks: These medusae look like a typical *Clytia hemisphaerica*. The only notable feature are the green radial canals. This alone, however, cannot be used as a diagnostic feature and it is likely variable as in other hydromedusae. It was not possible to identify the species with any *Clytia* from Florida mentioned in Mayer (1900, 1910). The hydroid stage of this species must first be found to allow a naming and complete description of the species.

? *Clytia* spec.2

Fig. 46D-G

Examined material: BFLA4253; 1 specimen; 23-NOV-2019; size 3 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence MW528694. – BFLA4257; 1 specimen; 23-NOV-2019; size 2 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528694. – BFLA4269; 1 specimen; 04-DEC-2019; size 4 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528694. – BFLA4274; 1 specimen; 04-DEC-2019; size 3 mm, with developing gonads; preserved in alcohol for DNA extraction; 16S sequence identical to MW528694. – 06-DEC-2019; 1 specimen, 6 mm, photographed, not collected; most probably also belongs to this species.

Observations: Umbrella 2 to 4 mm in diameter when gonad development starts, flatter than hemisphere when relaxed, mesoglea moderately thick, thinning towards margin. Manubrium small, urn shaped, with 4 (5?) short perradial lips, margin smooth. Gonads just developing in middle of complete radial canals and also on some incomplete ones. Complete radial canals thin, numbering 5 to 9, originating from manubrium, often irregularly spaced, rarely seen branched, some not entirely straight. With 0 to 15 incomplete centripetal canals originating from circular canal (Fig. 46D), usually from marginal bulbs but not always, not reaching manubrium, length variable from very short to about 3/4 of complete radial canal length. 16 to 22 tentacles arising from small conical bulbs, few atentacular bulbs (3-6) present. Usually 2 statocysts between pairs of bulbs, variable from 1 to 4. Colour: Most specimens without colour, one had pink bulbs. A specimen for which no 16S data is available, but which looked otherwise indistinguishable, had two manubria (Fig. 46G), one being smaller.

16S Data: The four sequenced specimens gave all the same 16S sequence (MW528694). In a maximum likelihood tree (not shown) obtained by comparing it to the Campanulariidae 16S dataset of Cunha *et al.* (2017) it came out as sister lineage to a clade tentatively identified as *Clytia* cf. *stolonifera* Blackburn, 1938 (GenBank KX665270, KX665268) in Cunha *et al.* (2017). The base pair divergence between KX665270 and MW528694 is 7.2%.

Remarks: While the 16S data clearly identified it as a Campanulariidae, finding the correct genus of this material was difficult and is still unsettled. A specimen with five radial canals (Fig. 46F) suggests that it could be *Pseudoclytia pentata* Mayer, 1900, but the presence of centripetal canals is not compatible with this species. Mayer (1910) found and examined an immense number of *P. pentata* over several years and the number of radial canals was somewhat variable, but he never observed centripetal canals. Mayer's medusae rarely had two manubria, just like in our case (Fig. 46G), although we have no 16S data for this specimen to assure that it is the same species as the others examined here.

Our 16S sequence was relatively similar to sequences obtained from two campanulariid hydroids from Belize that resembled the Australian *Clytia stolonifera* (see Cunha *et al.*, 2017). The observed divergence of 7.2% represent likely an interspecifc difference when compared to the values of Table 1, but with so few samples the value is currently inconclusive. In the phylogeny of Cunha *et al.* (2017), their hydroids did not cluster within the *Clytia* clade, but had an ambiguous phylogenetic position, frequently placed at the base of Obeliinae. This could mean that a genus other than *Clytia* may be needed for the specimens of Cunha *et al.* (2017) and also the medusa BFLA4253 of this study. DNA sequence information of the type species of *Pseudoclytia* and *Gastroblasta* must be obtained to resolve if one of these genera also belongs to this clade and could be the appropriate genus. For recent discussion of these genera see Gravili *et al.* (2007).

Genus *Gastroblasta* Keller, 1883

Gastroblasta Keller, 1883: 622; type species *Gastroblasta timida* Keller, 1883 by monotypy.

Diagnosis: Medusa when mature with more than one urn-shaped manubrium; up to 20 radial- and as many centripetal canals, some radial canals may be branched; marginal tentacles with bulbs; numerous statocysts, oval gonads developing near the middle of radial canals or also centripetal canals.

Hydroid like in genus *Clytia*, living embedded in sponges (Gravili *et al.*, 2007).

Gastroblasta timida Keller, 1883
Fig. 47A-C

Gastroblasta timida Keller, 1883: 622, pl. 35 figs 1-2. – Mayer, 1910: 279, fig. 151. – Kramp, 1961: 162. – Kramp, 1968: 75. – Gravili *et al.*, 2007: 400.

Examined material: 04-MAR-2019; 1 specimen photographed, not collected.

Observations: Bell diameter 6 mm, circular circumference, flatter than hemisphere, apex rather flat, jelly moderately thick, thickness rather even. Three manubria in middle region of bell, connected by the radiating corners of their bases, urn-shaped, mouth cruciform with four simple lips, not crenulated. 15 broad, band-like radial canals reaching circular canal, 12 incomplete centripetal canals originating from circular canal at the position of bulbs, reaching to variable height but not joined to manubrium. 70 large marginal bulbs with tentacles, tentacles long. About as many statocysts as bulbs. Gonads oval thickenings on radial- and centripetal canals, all about in middle of bell.

Remarks: This medusa matched rather well the description and figures of *Gastroblasta timida* given by Keller (1883) or Mayer (1910). The species was originally described from a number of specimens caught in the Red Sea, but has never been reported subsequently (Gravili *et al.*, 2007).

A closely related and better-known *Gastroblasta* species is the Mediterranean *G. raffaelei* Lang, 1886 (see Gravili *et al.*, 2007). It differs from *G. timida* in having a distinctly elliptical bell.

Multioralis ovalis Mayer, 1910 is the only known medusa species from the western Atlantic having multiple manubria. It has an oval bell and only a single radial canal, even when gonads begin to mature. Although it has been reported several times from different localities (Gravili *et al.*, 2007; Wang *et al.*, 2019), some authors like Kramp (1968) thought it to be an abnormal *Clytia*. Moreover, its structure corresponds to a stage in the development of *Gastroblasta raffaelei* (Gravili *et al.*, 2007).

Although structurally similar to the above described *Clytia* spec. 2 (Fig. 46D-G), the broad radial canals distinguish it immediately from it. Additionally, the general aspect and the tentacle number are different. Both share the presence of centripetal canals originating from tentacle bulbs. Some of them might later join the manubrium. In *Gastroblasta raffaelei* all but two opposite radial canals develop from centripetal canals (Gravili *et al.*, 2007).

We therefore hesitatingly attributed the present sample to *Gastroblasta timida*, despite the wide separation of the occurrences and the somewhat doubtful status of the species.

Distribution: Red Sea, Florida (this study). Type locality: Red Sea, Sudan, Suakin Harbour.

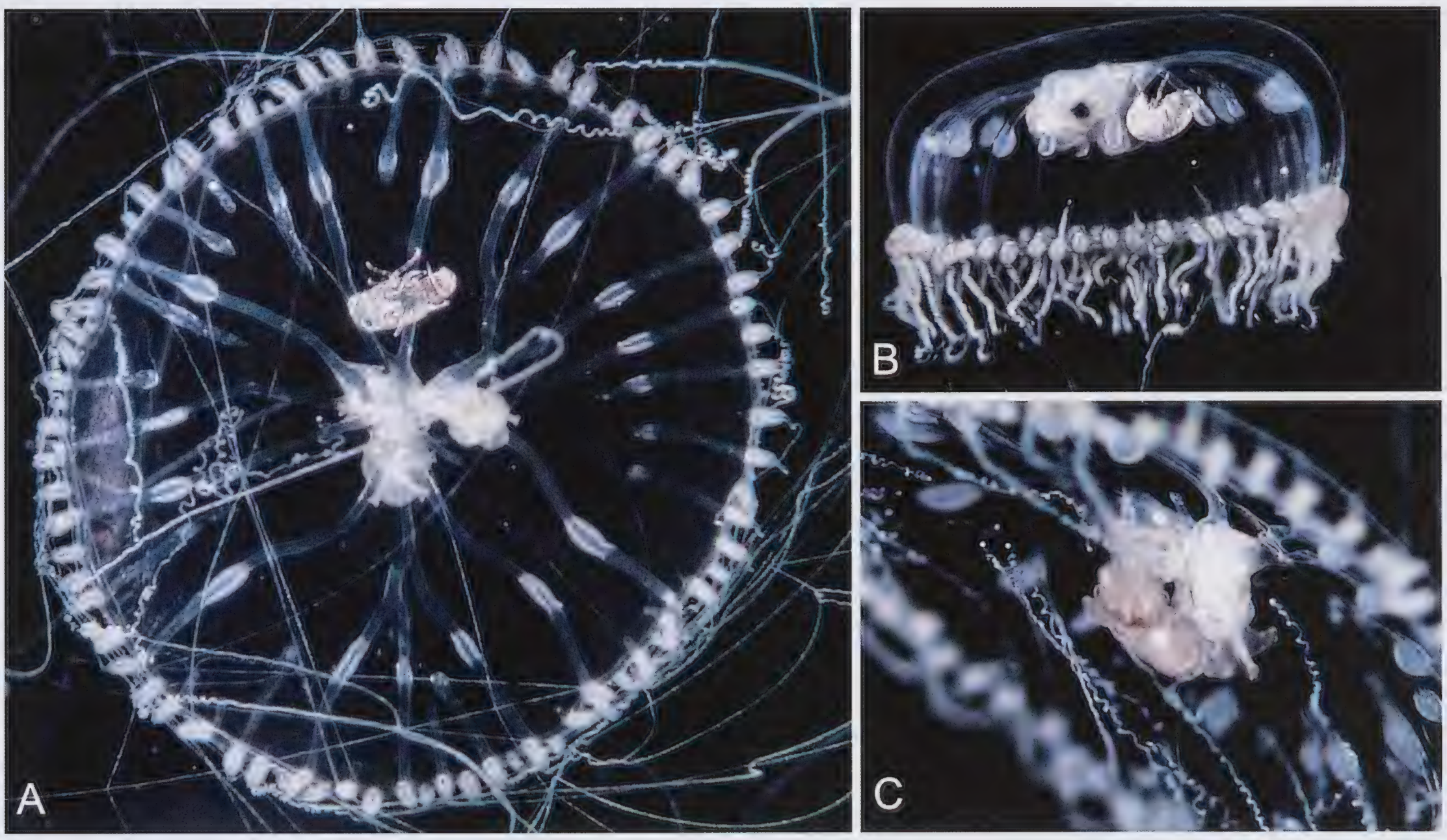


Fig. 47. *Gastroblasta timida*, diameter 6 mm, with crustaceans in subumbrella. (A) Whole animal. (B) Lateral view of contracted animal. (C) Close up of region with stomachs in lateral view.

Order Narcomedusae

Remarks: The families of the Narcomedusae have recently been reorganized by Lindsay *et al.* (2017) using DNA data. Bentlage *et al.* (2018) added more sequences. The 16S sequences of these studies and the ones from the present study were combined to get a maximum likelihood tree (Fig. 48). Although 16S has low resolving power above the genus level, some well supported nodes indicate that the Cuninidae and Solmarisidae are polyphyletic as already found by Bentlage *et al.* (2018). As revision of the families is beyond the scope of this study, we here used the family level taxonomy of Bouillon *et al.* (2006) and Lindsay *et al.* (2017), except for the genus *Otoporpa*.

Family Cuninidae Bigelow, 1913
Genus *Cunina* Eschscholtz, 1829

Cunina Eschscholtz, 1829: 116; type species *Cunina globosa* Eschscholtz, 1829 (Kramp, 1961).

Cunoctantha Haeckel, 1879: 31; type species *Cunina octonaria* McCrady, 1859 by designation of Mayer (1910: 460).

Diagnosis: Narcomedusae with as many undivided manubrial pouches as tentacles, gonads in these pouches, primary tentacles positioned in middle of the lower margin of the stomach pouches; with otoporpae, with or without peripheral canal system, without small secondary marginal tentacles.

Cunina becki Bouillon, 1985

Fig. 49A-F

Cunina becki Bouillon, 1985: 263, fig. 9.

Examined material: BFLA4022; 1 specimen; 15-FEB-2019; size 14 mm; preserved in formalin and deposited as UF-013444. – BFLA4023; 1 specimen; 15-FEB-2019; size 20 mm; preserved in formalin and deposited as UF-013444. – BFLA4025; 1 specimen; 15-FEB-2019; size 20 mm; part preserved in formalin and deposited as UF-013446, 1/4 part in alcohol for DNA extraction; 16S sequence MW528643.

Observations: Medusae flatter than hemisphere, 14 to 20 mm in diameter, jelly very soft and fragile, margin lobed. Stomach flat, circular, about 1/3 of bell diameter, mouth opening simple, circular (Fig. 49A). 16 band-like manubrial pouches radiating from stomach to the bell margin, pouches slightly widening to about 3/5 of their length, then gradually narrowing again before dividing above tentacle into two narrow peripheral canals or strands (Fig. 49E). The proximal 3/5 of the gastric pockets are more opaque (Fig. 49D) than the rest as the bottom contains the gonad tissue, in the present cases containing numerous, densely packed, small (16 µm), round cells interpreted as oogonia. Tentacles 16, between pairs of tentacles 4 to 7 otoporpae clasping bell margin (Fig. 49E). No peronia.

16S data: The sole 16S sequence clustered within a clade comprising Narcomedusae of different families (Fig. 48).

Distribution: Papua New Guinea, Florida (this study). Type locality: West Pacific, Bismarck Sea, Hansa Bay.

Remarks: *Cunina becki* has so far only been recorded from its type locality in the Bismarck Sea (western Pacific Ocean). It was thus very surprising to find it in the western Atlantic Ocean. The species may have been overlooked as it has a very fragile jelly, which might not withstand usual net collecting. *Cunina becki* is rather unusual for its genus – or even all Narcomedusae – in that the gastric pockets are very narrow and extend to the bell margin, resembling thus radial canals of other hydromedusae. While the main diagnostic features of our medusae – long and narrow gastric pockets, otoporpae, and peripheral canal or strand – match the description given in Bouillon (1985), there are nevertheless some slight differences:

- larger diameter (20 versus 15 mm)
- 16 gastric pockets and tentacles (versus 12-15)
- 4-7 otoporpae between successive tentacles (versus 3-4)
- the gastric pockets narrow gradually distal to the gonads (versus rather abrupt).

Considering the variability of other *Cunina* species (see e. g. Kramp, 1959a, 1968), we think that these differences are due to intraspecific variations and mainly correlated to the somewhat larger size.

With the available material it was not possible to decide if the peripheral canal is really a canal or just a tissue strand. Histological sections are needed to answer this.

Cunina octonaria McCrady, 1859

Fig. 50A-D

Cunina octonaria McCrady, 1859: 211, pl. 12 figs 4-5. – Kramp, 1959a: 199, fig. 307. – Kramp, 1961: 282, synonymy, references. – Kramp, 1968: 128, fig. 347. – Calder, 1971: 77, pl. 8I. – Goy, 1979: 286, fig. 28. – Bouillon, 1987: 197, figs 4A-B, 7A, photos 2-4. – Bouillon *et al.*, 1988a: 223. – Bouillon, 1999: 433, fig. 3.150. – Bouillon *et al.*, 2004: 234, figs 144E, 145A, 149A-H. – Galea, 2007: 97, fig. 21O. – Nogueira, 2012: fig. 15. – Nagata *et al.*, 2014: 312, figs 31-32.

Cunina koellikeri Müller, 1861a: 41, pl. 4.

Foveolia octonaria. – A. Agassiz, 1865: 51.

Cunoctanthanparasitica Metschnikoff, 1882: 442.

Cunocantha octonaria. – Brooks, 1886: 361, pls 43-44, life cycle. – Mayer, 1910: 461, text figs 304-305, pl. 55 figs 1-2.

Cunoctantha octonaria var. *köllikeri*. – Mayer, 1910: 464, pl. 54 figs 4-9.

Examined material: 27-May-2019; 1 specimen photographed, not collected; size 7 mm, with beginning gonad maturation. – 27-NOV-2019; 1 specimen photographed, not collected; size 4 mm.

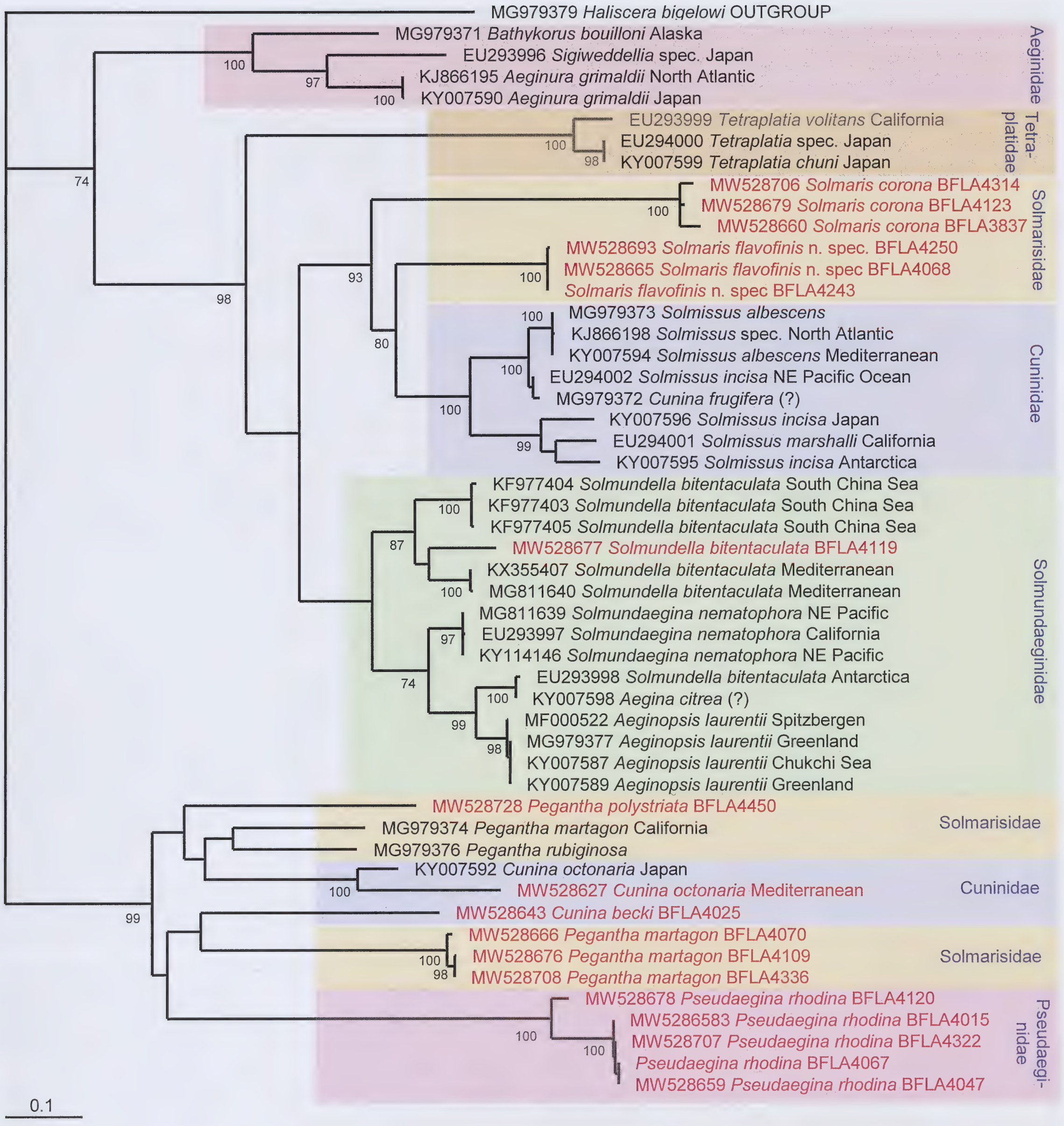


Fig. 48. Maximum likelihood phylogenetic tree of Narcomedusae obtained with PhyML (GTR+G+I model) and based on about 600 bp positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Sequence labels start with the GenBank numbers (except for identical haplotypes) permitting the retrieval of more information. Some proveniences were obtained from Lindsay *et al.* (2017) or through personal communications. Red labels are new sequences from this study. Coloured boxes indicate family affiliations according to the currently used system. (?) Denotes possible misidentifications.

Mediterranean, France, Bay of Villefranche-sur-Mer, 43.6860°N 7.3170°E, depth 0-70 m; 1 specimen collected 24-APR-2016, used for DNA extraction, 16S sequence MW528627.

Observations: Florida specimens up to 7 mm in diameter, somewhat flatter then hemispherical (Fig. 50B), stomach circular, about half the diameter of bell, without mesoglea cone, with eight broad, manubrial pockets shaped like an isosceles trapezium, region between pockets narrow, band-shaped (Fig. 50A). Eight tentacles originating in middle of pocket base with a short, conical root (Fig. 50C);

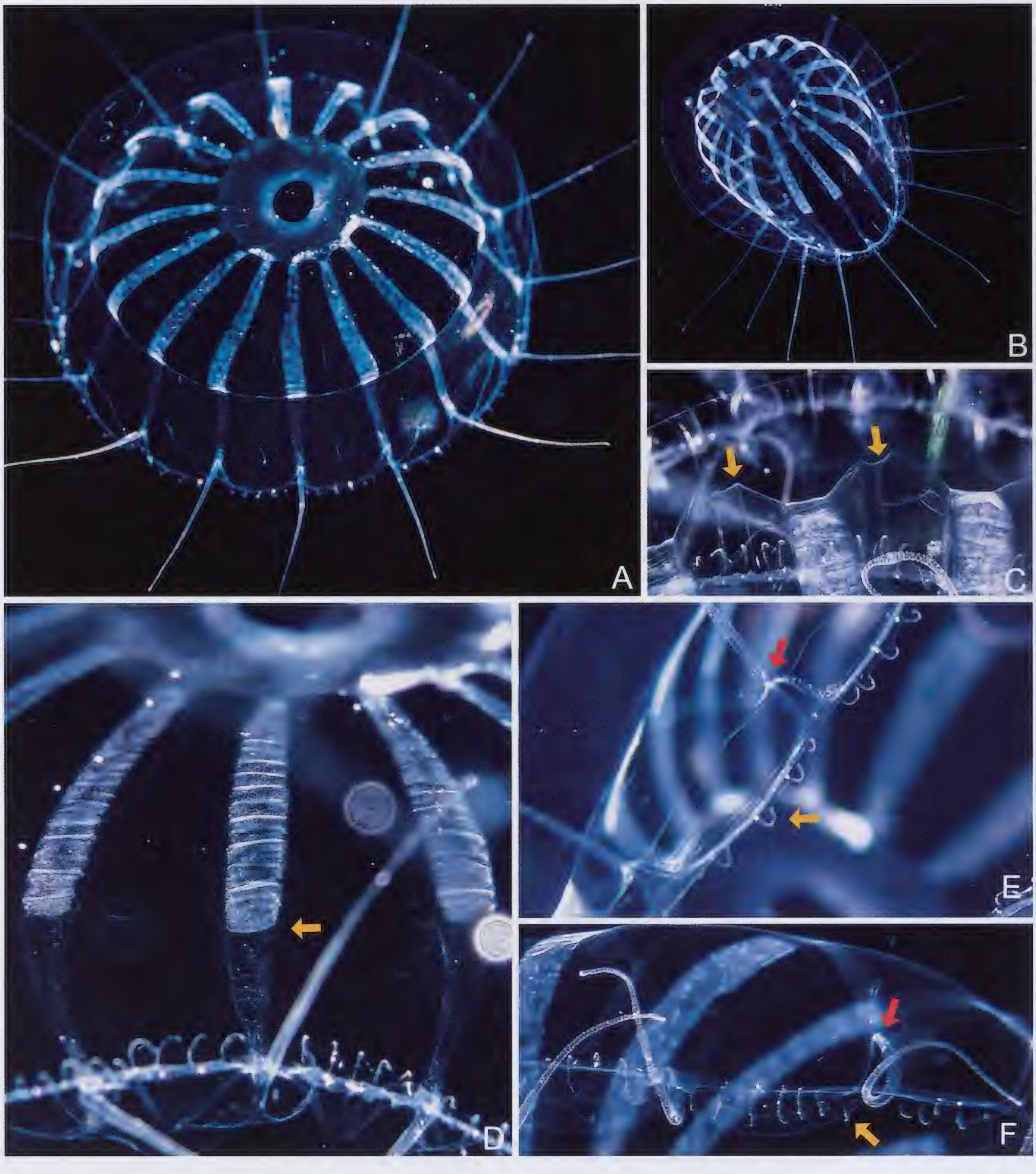


Fig. 49. *Cunina becki*. (A) Aboral view of whole animal, sample BFLA4022, diameter 14 mm. (B) Medusa in contraction phase, sample BFLA4025. (C) BFLA4023, side view showing optical cross-section through gastric pockets (secant plane of bell), oral side is downwards, arrows indicate the lateral margins of one gastric pocket. (D) Gastric pockets seen from above, note transition from the opaque zone with the developing gonads to clear part (arrow). (E-F) BFLA4022, bell margin showing several otoporpae per lappet (yellow arrows) and the bases of tentacles (red arrows).

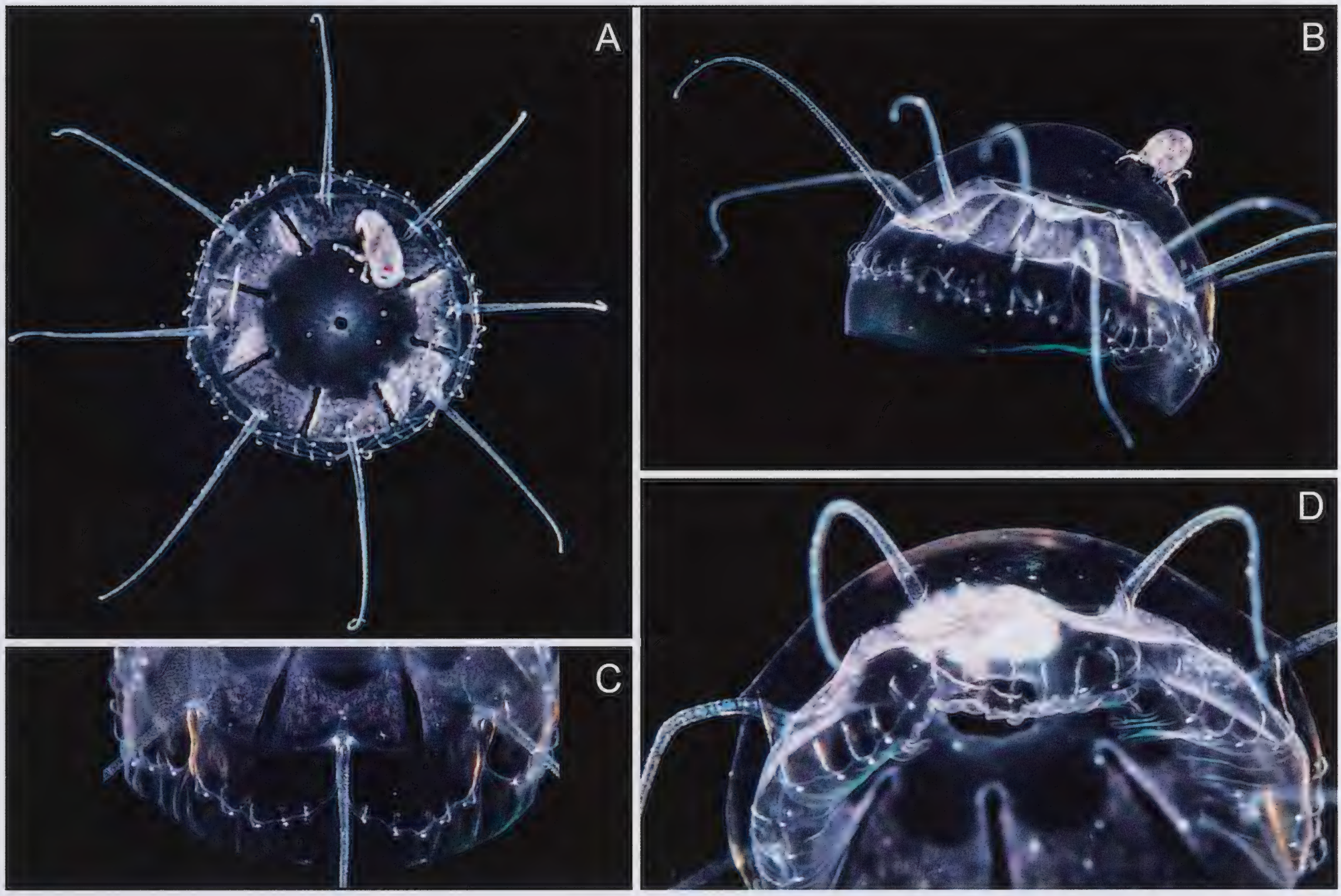


Fig. 50. *Cunina octonaria*, diameter 7 mm. (A) Aboral view of whole animal, with a crustacean on exumbrella. (B) Lateral view. (C) Close up of bell margin, note otoporpae and root of tentacle in middle, the velum is hanging downwards. (D) Oblique view from oral side. The bright spots below the otoporpae are the statocysts.

tentacles projecting from exumbrella at about ¼ between margin and apex of bell. Bell margin between pairs of tentacles lobed, with 4-5 otoporpae and statocysts.

Distribution: Widely distributed in tropical and warm-temperate parts of all oceans, including also the Mediterranean, the Chilean coast, and the South Atlantic (Kramp, 1968; Bouillon, 1999; Bouillon *et al.*, 2004; Galea, 2007; Nagata *et al.*, 2014). Type locality: USA, South Carolina, Charleston Harbor.

Remarks: No DNA samples could be obtained for the Florida specimens. The Mediterranean specimen differed in having 9 or 10 tentacles and pouches (damaged), one statocyst and otoporpe per lappet, manubrial pouches U-shaped.

Family Pseudaeginidae Lindsay, Bentlage & Collins, 2017

Pseudaeginidae Lindsay, Bentlage & Collins, 2017, in Lindsay *et al.*, 2017: 507.

Genus *Pseudaegina* Lindsay, 2017

Pseudaegina Lindsay, 2017 in Lindsay *et al.,* 2017: 507, type species *Aegina rhodina* Haeckel, 1879 by original designation.

Diagnosis: Narcomedusae with interradial manubrial pouches which are subdivied by a short septum in the middle; with peripheral canal system; with primary perradial tentacles alternating with pairs of marginal pouches; tentacle roots recurved orally without penetrating deep into central mesoglea; manubrial pouches begin at points of origin of primary tentacles; deep peronial grooves lined with nematocysts below but not above points of origin of primary tentacles; without secondary tentacles on umbrella margin; without otoporpae.

Pseudaegina rhodina (Haeckel, 1879)

Fig 51A-G, Fig. 52A-B

Aegina rhodina Haeckel, 1879: 338, pl. 20 figs 11-15. – Mayer, 1904: 27, pl. 4 figs 28-29. – Maas, 1905: 71, is Atlantic species. – Mayer, 1910: 452, plate 52, fig. 5; plate 54, figs 11, 11'-11'".

Aegina canariensis Haeckel, 1879: 339. – Maas, 1905: 71, synonym of *A. rhodina*. – Mayer, 1910: 452, synonym.
Aegina eschscholtzi Haeckel, 1879: 339. – Maas, 1905: 71, synonym of *A. rhodina*. – Mayer, 1910: 453.
Solmundus tetralinus Haeckel, 1879: 351. – Maas, 1905: 71, synonym of *A. rhodina*. – Mayer, 1910: 452, synonym of *A. rhodina*.
? *Aegina lactea* Vanhöffen, 1908: 50, pl. 1 fig. 3.
Aegina citrea. – Bleeker & Van der Spoel, 1988: 244, figs 43-44. – Larson *et al.*, 1989: 789. – in part Kramp, 1959a: 61. [not *Aegina citrea* Eschscholtz, 1829]
Pseudaegina rhodina. – Lindsay *et al.*, 2017: 507, figs 11-13, redescription, new combination.

Examined material

Specimens with 5 tentacles: BFLA4015; 1 specimen; 17-JAN-2019; size 18 mm; part preserved in formalin and deposited as UF-013441, small part in alcohol for DNA extraction; 16S sequence MW528658. – BFLA4047; 1 specimen; 01-APR-2019; size 16 mm; part preserved in formalin and deposited as UF-013451, small part in alcohol for DNA extraction; 16S sequence MW528659. – BFLA4067; 1 specimen; 10-APR-2019; size 20 mm; part preserved in formalin and deposited as UF-013778, small part in alcohol for DNA extraction; 16S sequence identical to MW528659. – BFLA4322; 1 specimen; 24-JAN-2020; size 15 mm; part preserved in formalin and deposited as UF-013887, small part in alcohol for DNA extraction; 16S sequence MW528707. – 13-MAR-2020; 1 specimen; 15 mm; not collected.
Specimens with 4 tentacles: BFLA4120; 1 specimen; 04-JUN-2019; size 9 mm; part preserved in formalin and deposited as UF-013803, small part in alcohol for DNA extraction; 16S sequence MW528678. – BFLA4134; 1 specimen; 15-JUN-2019; size 11 mm; part preserved in formalin and deposited as UF-013809, small part in alcohol for DNA extraction; 16S sequence not determinable. – BFLA4118; 1 specimen; 04-JUN-2019; size 9 mm; part preserved in formalin and deposited as UF-013809, small part in alcohol for DNA extraction, not examined.

Observations

Form with 5 tentacles: Umbrella approximately hemispherical, 15-20 mm, jelly firm, apical mesoglea half the bell height, tentacles issue at about 2/3 of bell height, above tentacles a small bulge (Fig. 51A-B). Velum broad (Fig. 51A). Stomach about half the bell diameter, mounted on a rounded mesogleal cone of the same diameter reaching to level of bell margin (Fig. 51A). Mouth rim can form temporary folds or even a tubular extension with terminal folds (Fig. 51D-F). Five subdivided manubrial pockets (Fig. 51C-D). Manubrial pockets broadly U-shaped, reaching from stomach rim to about half the distance to bell margin (Fig. 51A), in middle a narrow septum which does not reach to the stomach level or level of tentacle origin (Fig. 51C, smp). At bottom of left and right side of the pairs of pouches originates a broad peripheral canal, directed first along peronium towards the bell margin and then following the latter (Fig. 51C). Five tentacles originating in upper half of medusa at about upper level of stomach, the proximal end embedded in an exumbrellar furrow, the tentacle roots rather short, entering the mesoglea, tapering, and curved towards oral (Fig. 51B); tentacle length about 2-3 bell diameters, curved towards oral, nematocysts concentrated on upper side but also present on underside. Below tentacles a deep cleft in exumbrella reaching down to bell margin, its floor with a thickened epidermis containing nematocysts (= peronium, Fig. 51C-G). 48 to ca. 68 statocysts. No otoporpae. Almost colourless, greenish or yellowish cast in daylight.
Form with 4 tentacles: As above, but only four tentacles and four pairs of manubrial pouches, size 9 to 11 mm, 36 to 60 statocysts.

16S data: In the maximum likelihood tree (Fig. 48), all five samples clustered in a lineage that was well separated from most other Narcomedusae. The clade had a distinct internal dichotomy with the single 4-tentacled specimen being rather apart from the 5-tentacled medusae (7.6 to 7.8% base pair differences). The three haplotypes of the 5-tentacled medusae were rather similar (0.18-0.36% divergences, Table 1).

Distribution: Tropical to subtropical Atlantic Ocean (Lindsay *et al.*, 2017). Type locality: Canary Islands, Lanzarote.

Remarks: Haeckel's type material of this species consisted in three specimens. Two of them had four tentacles and a size of 40 mm, one had five tentacles and measured 50 mm. He depicted a mature female with four tentacles. The statocyst numbers were given as two per manubrial hemi-pouch (16-20 in total).
Kramp (1955b, 1961) synonymized this species with the similar *Aegina citrea* Eschscholtz, 1829, an opinion already pondered by Mayer (1910). This view was upheld until Lindsay *et al.* (2017) revised *Aegina citrea* and split it into several species and belonging to separate families, this based on morphological and genetic differences. The main morphological difference to *Aegina* is the shape of the tentacle root. In *Aegina* they are curved towards aboral, in *Pseudaegina* they are curved towards oral.
Our specimens with 5 tentacles matched the description of Lindsay *et al.* (2017) very well as they came from the same region. There are, however, some differences to Haeckel's description. Our specimens were smaller (up to 20 mm) but all immature. The most obvious difference is the number of statocysts: Haeckel saw about 16-20, while we found regularly 60-68.
The haplotype divergence in our sample was high (p-value up to 7.8%) and in the maximum likelihood tree the samples split into two sub-clades (Fig. 48). This separation coincided with two morphotypes: the four- and five-tentacled form (see above). Unfortunately, we could get only one sequence of the four-tentacled form and due

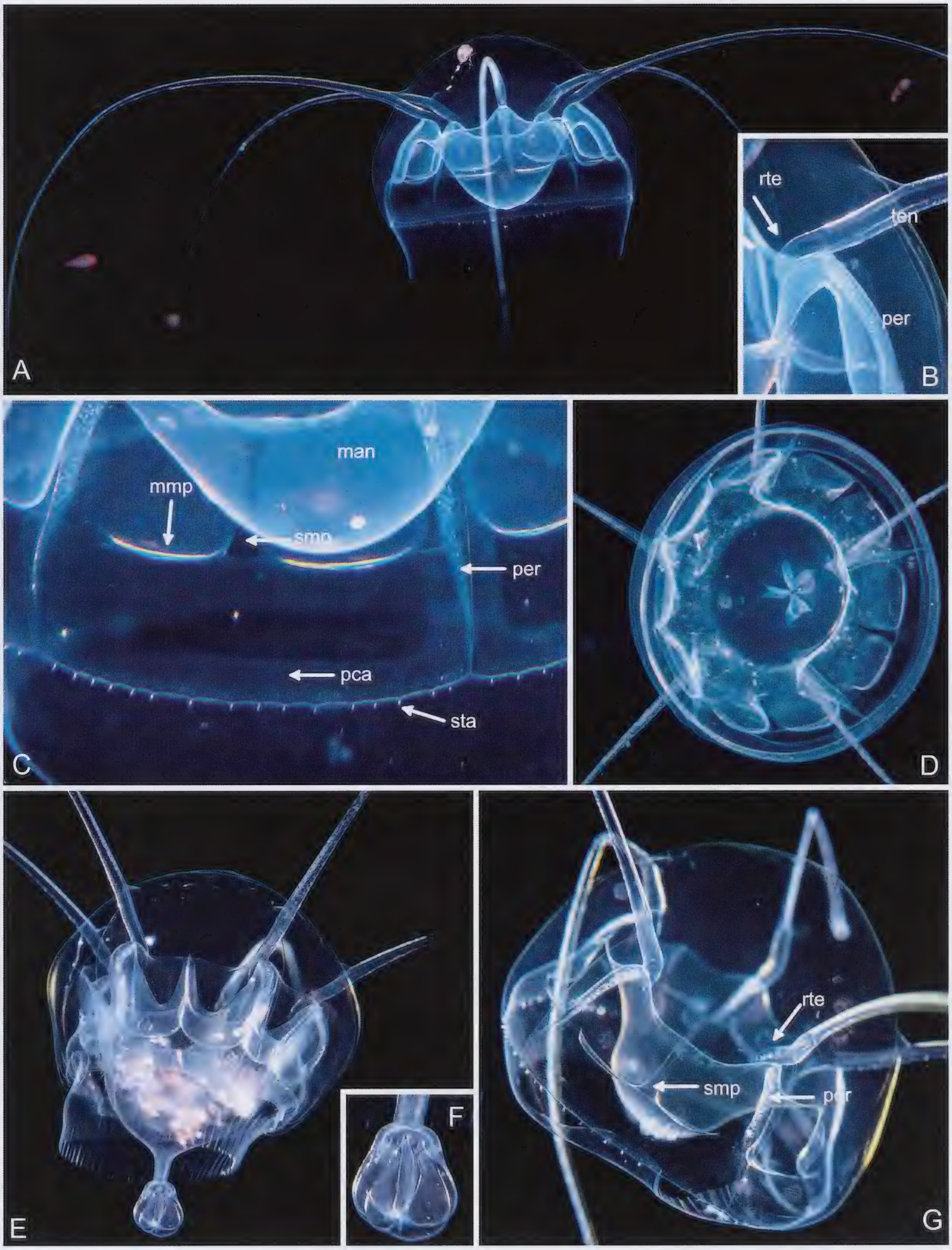


Fig. 51. *Pseudaegina rhodina* with 5 tentacles. (A-C) BFLA4015, size 18 mm. (D) BFLA4047, size 16 mm. (E-F) BFLA4067, size 20 mm. (G) BFLA4322, size 15 mm. (A) Lateral view. (B) Higher magnification of tentacle root (rte, arrow), note inflection towards below (= oral). (C) Details of bell margin. (D) Aboral view, note the (temporary) folding of mouth margin. (E-F) Medusa which has recently fed and its stomach is full of prey. Note the particular, most likely transitory, formation of a mouth tube and folded mouth margin, shown at higher magnification in F. (G). Lateral view. Abbreviations: man – manubrium/stomach covering conical jelly cone, mmp – distal margin of manubrial pouch, pca – peripheral canal, per – peronium, rte – tentacle root, smp – septum in middle of manubrial pouch, sta – statocyst.

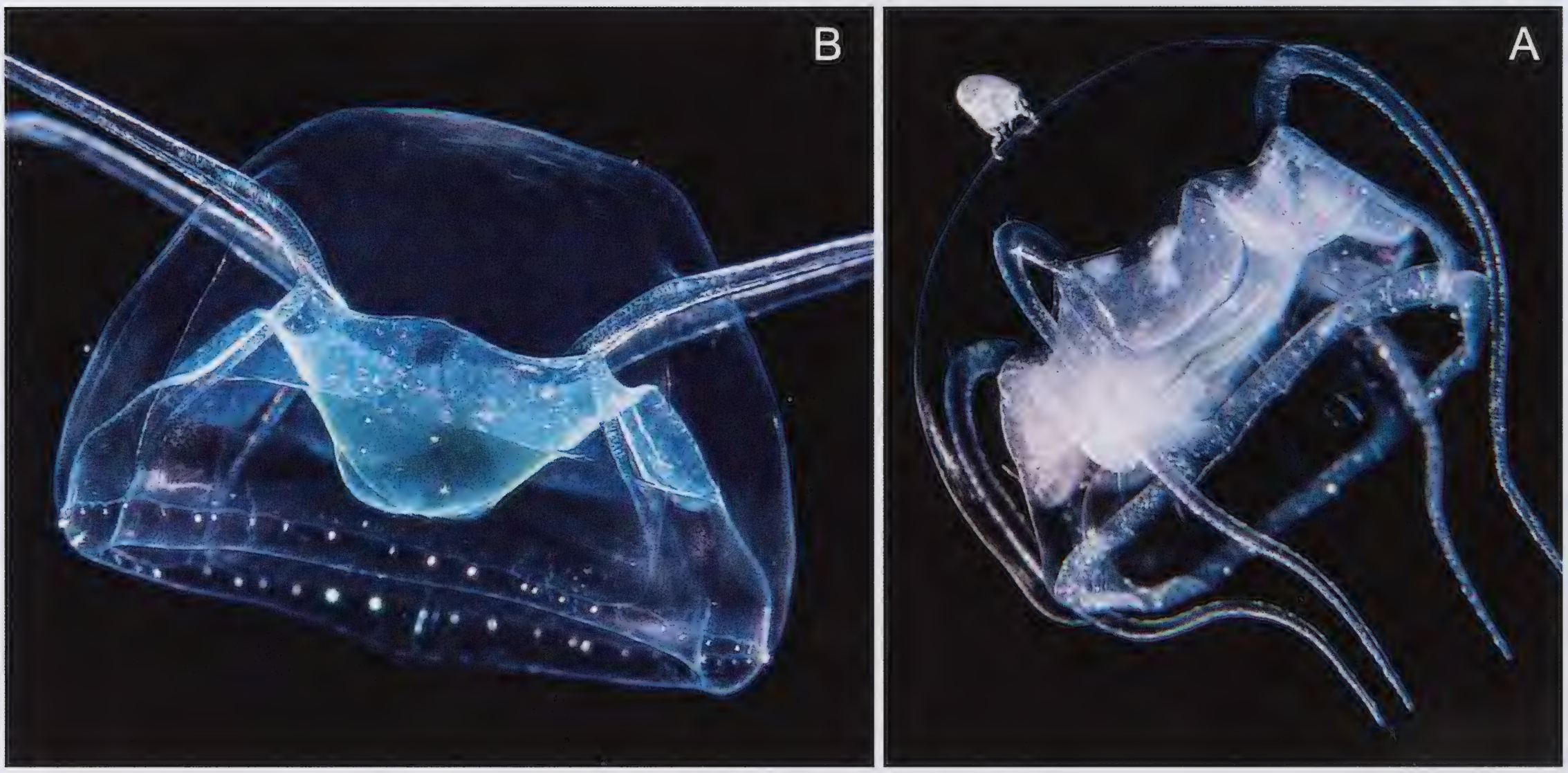


Fig. 52. *Pseudaegina rhodina* with 4 tentacles. (A) BFLA4134, size 9 mm, animal has semi-digested prey items in its gastric system including the peripheral canal system rendering it thus much more visible. (B) BFLA4120, bell size 9 mm, lateral view.

to the low number of samples, this distribution could also be due to mere contingency. The four-tentacled medusae were all smaller than those with five tentacles and it is nevertheless the possible that our material was composed of two sister-species. Because the original material of Haeckel included both four- and five-tentacled forms, it is not possible to use the tentacle number in the diagnosis of a new species without the designation of a lectotype (or a neotype as Haeckel's material is likely lost). A population-genetic study at the type locality combined with the designation of a neotype is thus needed to resolve this taxonomic problem. Because of these unresolved issues and because our samples were monophyletic, we felt it premature to describe one of the clades as a new species.

One particularity not mentioned in previous descriptions concerns the temporary folds of the mouth region (Fig. 51D-F). One of the figures in Lindsay *et al.* (2017: fig. 12C) also shows this ruffling of the mouth margin. In one of our animals the mouth was even drawn out to a tube ending in a flower-like, folded mouth region. The folds disappeared after fixation. It is thus unlikely that they can ever be seen in standard net-plankton samples.

Family Solmarisidae Haeckel, 1879
Genus Pegantha Haeckel, 1879

? *Pegasia* Péron & Lesueur, 1810: 340, type species *Pegasia dodecagona* Péron & Lesueur, 1810 by designation of Haeckel (1879).

? *Polyxenia* Eschscholtz, 1829: 118; type species *Polyxenia cynostylis* Eschscholtz, 1829 by monotypy.

Eurystoma Kölliker, 1853: 322, invalid homonym of *Eurystoma* Rafinesque, 1818 and others.

Pegantha Haeckel, 1879: 332; type species *Pegantha martagon* Haeckel, 1879 (Kramp, 1959a).

Pegantha (*Peganthella*) Haeckel, 1879: 332, no type species designated.

Pegantha (*Peganthissa*) Haeckel, 1879: 332, no type species designated.

Polycolpa Haeckel, 1879: 327, no type species designated. – Kramp, 1957c: 65, synonym.

Solmoneta Haeckel, 1879: 353, no type type species designated. – Mayer, 1910: 439, synonym.

Otoporpa Xu & Zhang, 1978: 50; type species *Otoporpa polystriata* Xu & Zhang, 1978 by original designation. **n. syn.**

Diagnosis: Narcomedusae without manubrial pouches; with peripheral canal system; with gonads on periphery of stomach, ring-like, or covering bulges of the mesoglea, or pendant diverticula; with numerous tentacles leaving exumbrella at the level of manubrium attachment to subumbrella. With otoporpae.

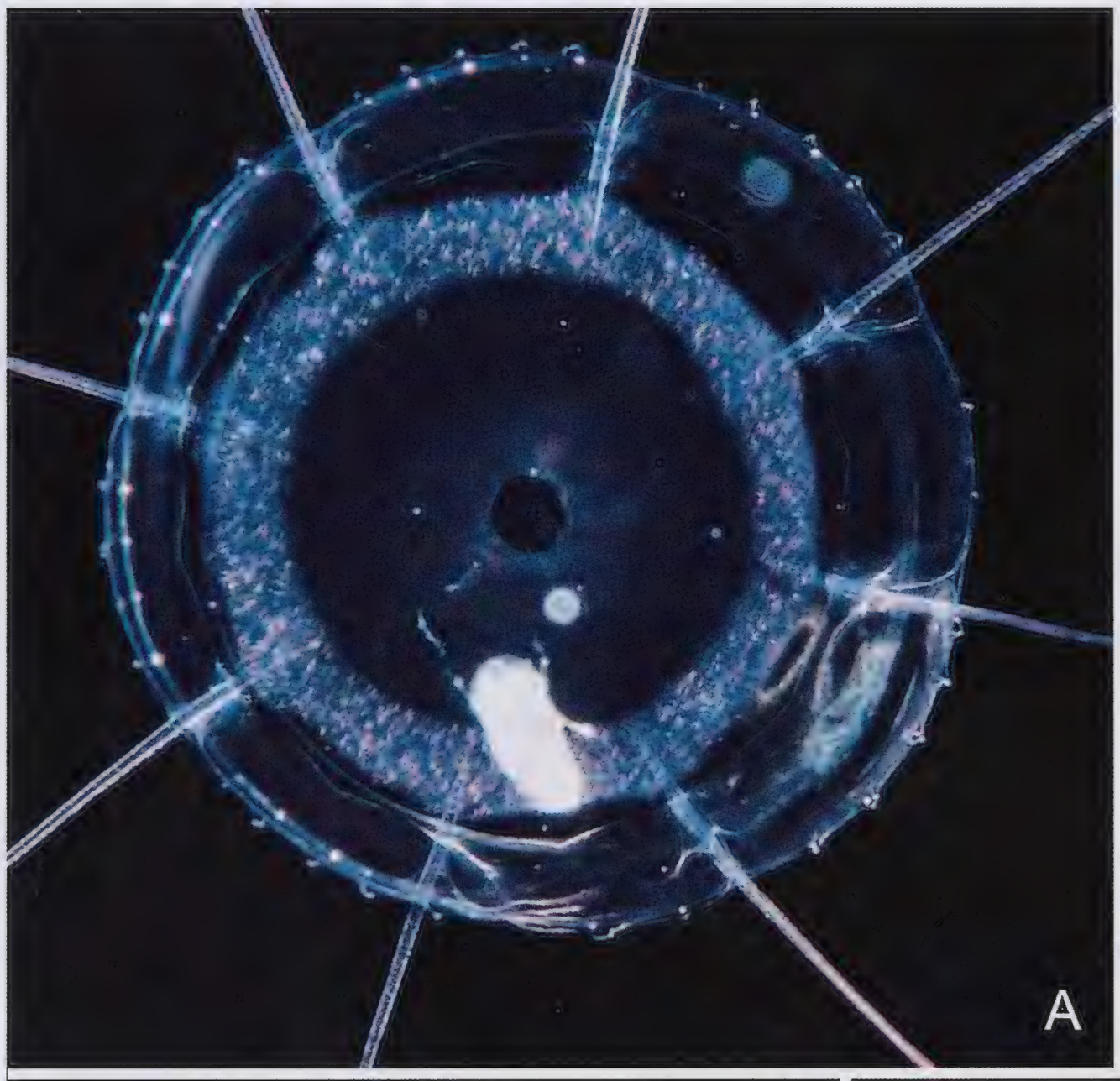
Remarks: The genus *Otoporpa* Xu & Zhang, 1978 is here regarded as synonym of *Pegantha*. For more details see below under *P. polystriata.*

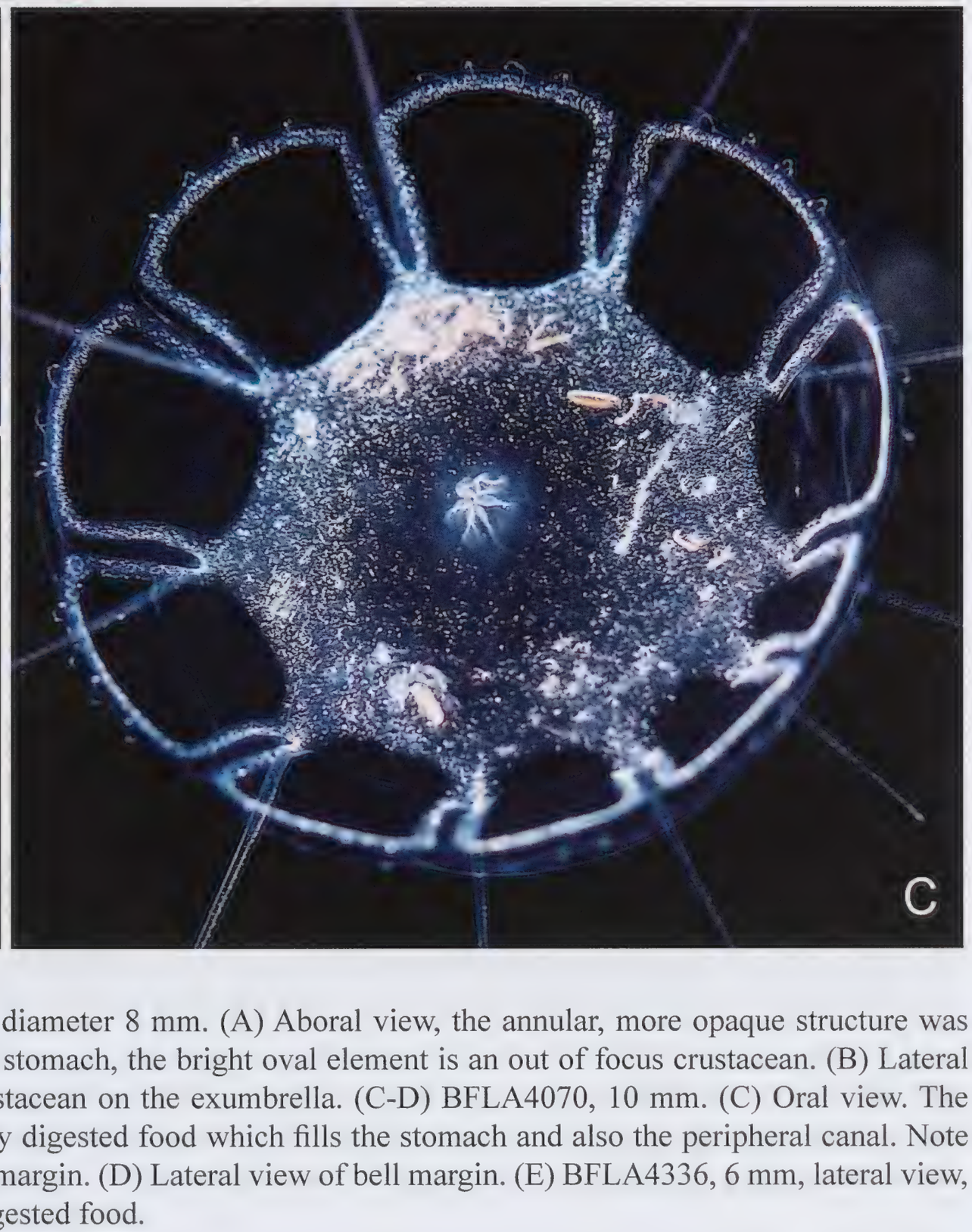
Pegantha martagon Haeckel, 1879
Fig. 53A-C

Pegantha martagon Haeckel, 1879: 332.

Polycalpa zonaria Haeckel, 1879: 327, Mediterranean.

? *Pegantha simplex* Bigelow, 1904: 260, pl. 5 figs 19-20. – Bigelow, 1909: 83.– Bigelow, 1918: 395, synonym of *P. martagon.*





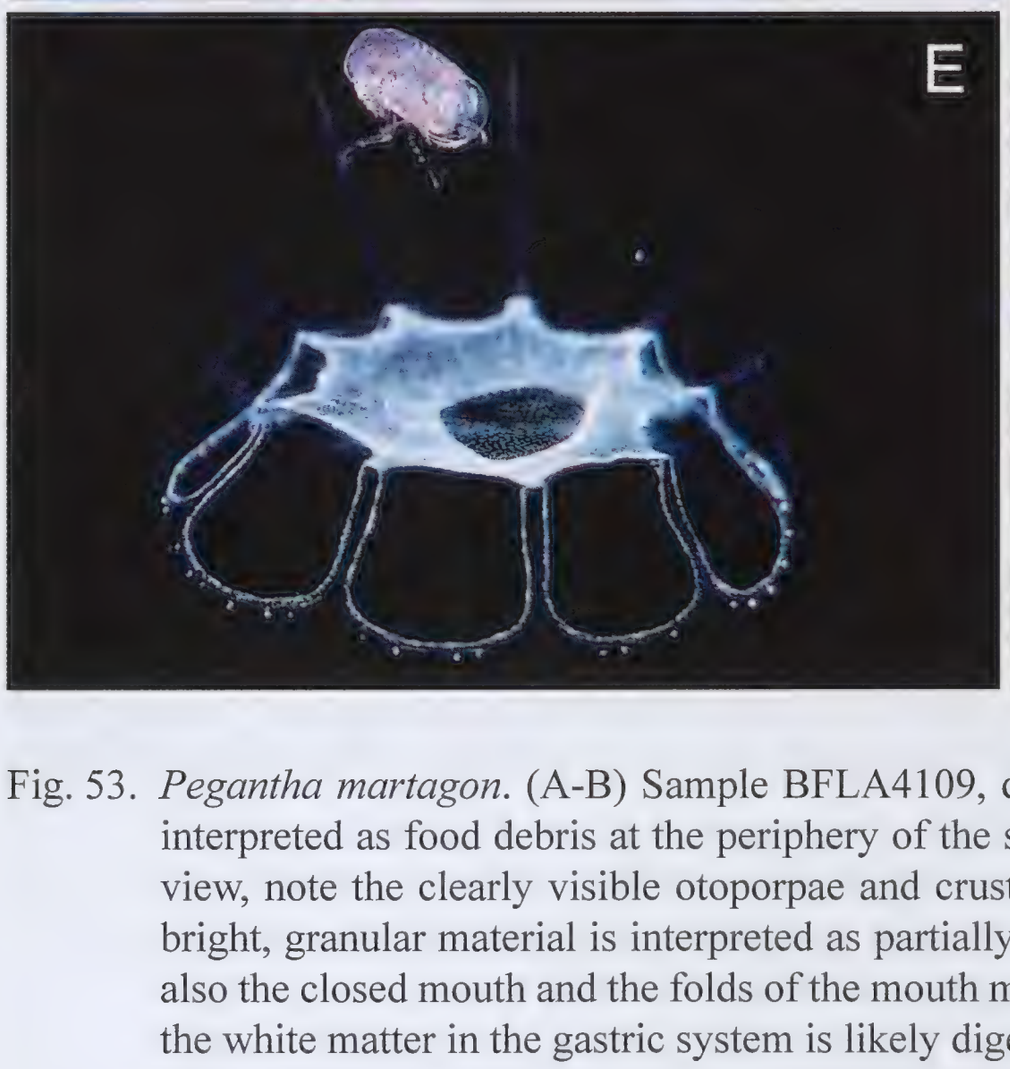


Fig. 53. *Pegantha martagon*. (A-B) Sample BFLA4109, diameter 8 mm. (A) Aboral view, the annular, more opaque structure was interpreted as food debris at the periphery of the stomach, the bright oval element is an out of focus crustacean. (B) Lateral view, note the clearly visible otoporpae and crustacean on the exumbrella. (C-D) BFLA4070, 10 mm. (C) Oral view. The bright, granular material is interpreted as partially digested food which fills the stomach and also the peripheral canal. Note also the closed mouth and the folds of the mouth margin. (D) Lateral view of bell margin. (E) BFLA4336, 6 mm, lateral view, the white matter in the gastric system is likely digested food.

Pegantha martagon. – Mayer, 1910: 443, figs 295-296. – Bigelow, 1909: 83, pl. 18 figs 1-8. – Bigelow, 1918: 396. – Kramp, 1955a: 160. – Kramp, 1957: 67, pl. 6 fig. 1, revision. – Kramp, 1959a: 64, 197, fig. 302. – Kramp, 1961: 274. – Kramp, 1968: 127, fig. 342. – Segura-Puertas, 1984: 45, pl. 14 fig. 1. – Pagès *et al.*, 1992: 41, fig. 49. – Larson *et al.*, 1989: 789, fig. 1A.

Examined material: BFLA4070; 1 specimen; 11-APR-2019; size 10 mm, 10 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528666. – BFLA4109; 1 specimen; 03-JUN-2019; size 8 mm, 8 tentacles; part preserved in formalin and deposited as UF-013796, small part in alcohol for DNA extraction; 16S sequence MW528676. – BFLA4336; 1 specimen; 07-FEB-2020; size 6 mm, 9 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528708. – 26-FEB-2018; 1 specimen photographed, not collected, 9 tentacles.

Observations: Medusae hemispherical or slightly wider than high, diameter 6-10 mm, 8-10 tentacles and marginal lappets (Fig. 53A, C, E), stomach wide, up to 2/3 of bell diameter, no gastric jelly cone (Fig. 53B, E), without manubrial pockets, peripheral canals originating below tentacles (Fig. 53C), first descending parallel along the peronial fold, then along lappet periphery, rather thin (1/6 of lappet width), width constant. Marginal lappets rectangular to rounded, with 4-5 otoporpae (Fig. 53B), these short, max. twice the size of the width of the peripheral canals. Statocysts near otoporpae, about as many as otoporpae. Tentacles curved, tapering, held at approximately 45° upwards, proximal end pointed and horizontal; below tentacles a slight furrow in the exumbrella with the peronium (Fig. 53A).

16S Data: The three obtained haplotypes have only low sequence divergences (Table 1, Fig. 48), but there was no significant relationship to a sequence of *P. martagon* from the Eastern Pacific (GenBank MG979374, Fig. 48).

Distribution: Widely distributed in the tropical and subtropical parts of the Atlantic and Indo-Pacific Ocean (Bigelow, 1909; Kramp, 1959a; Bouillon, 1978c; Bleeker & Van der Spoel, 1988; Navas-Pereira & Vannuci, 1991; Bouillon & Barnett, 1999; Segura Puerta *et al*., 2003, 2009; Oliveira *et al.,* 2016), surprisingly also in the cold waters around South Georgia and in Antarctic waters (Kramp, 1959a; Toda *et al.*, 2008). Occurs in shallow waters, occasionally from 100 to 300 m depth (Kramp, 1957). Type locality: China Sea.

Remarks: Our samples had apparently not yet developed gonads, being thus not fully mature. The observed tentacle numbers of 8-10 were lower than the 16 given in Kramp (1959a, 1968), but this is a maximal number and most animals have actually only 10-13 tentacles and lappets (Bigelow, 1909; Kramp, 1957, 1959a). According to Bigelow (1909) and Kramp (1959a: 64), the final tentacle number (10-11) is attained early in development, though during further growth some few tentacles and lappets may occasionally be added.

Kramp (1957) observed that the lateral portions of peripheral canal in the lappets are broader than the transverse portions along the bell margin. This was not seen in the present material (Fig. 53C-E).

Pegantha simplex Bigelow, 1904 – a nominal species based on a type specimen from the Maldive Islands – was later synonymized with *Pegantha martagon* by Bigelow himself (Bigelow, 1909, 1918). We think that Bigelow's specimen from the Maldives nevertheless deviates quite strongly from the scope of *P. martagon* as described by later authors (see synonymy above). It was a small (3 mm) medusa but with fully developed, pendant-sac-like gonads. It had 8 tentacles/lappets and reportedly 25 statocysts per lappet, more than twice the number usually seen in *P. martagon*. Later, Bigelow (1909) re-examined this material and had to revise this number. The contraction of the alcohol preserved material feigned the presence of more statocysts. Actually, also Haeckel (1879) in his first description reported 13-15 statocysts per lappet. Because he also had preserved material, Bigelow (1909) assumed that he was likewise mistaken.

The gonads of *P. martagon* are variably described as a simple ring at the periphery of the stomach, or as irregularly lobed, pendant sacs. While it is possible that these two stages are only different developmental stages, we nevertheless suspect that the wide variation of the current concept of *P. martagon* indicates that it comprises several species. Our 16S sequences are very different from a tentatively identified *P. martagon* from California found parasitizing a planktonic polychaete *Tomopteris* (Bentlage *et al.*, 2018).

Pegantha polystriata (Xu & Zhang, 1978) new comb.

Fig. 54A-G

Otoporpa polystriata Xu & Zhang, 1978: 50, pl. 12 figs 65-67.

Examined material: BFL4450; 1 specimen; 08-JUN-2020; size 5 mm; preserved in alcohol for DNA extraction; 16S sequence MW528728. – 02-SEP-2020; 1 specimen photographed, not collected, 2 mm. – Photos of two specimens kindly provided by Linda Ianniello, taken 21-MAR-2020 and 15-SEP-2020 during the same series of dives as for the other medusae of this study.

Observations: Bell diameter 5 mm, solid jelly, thickened aborally, margin subdivided in 8 to 9 U-shaped lappets (Fig. 54A, E), at margin of lappets 3 to 5 statocysts from which originate otoporpae (tracks of thickened epidermis with nematocysts, Fig. 54B, G) that extend almost to bell apex (Fig. 54B),

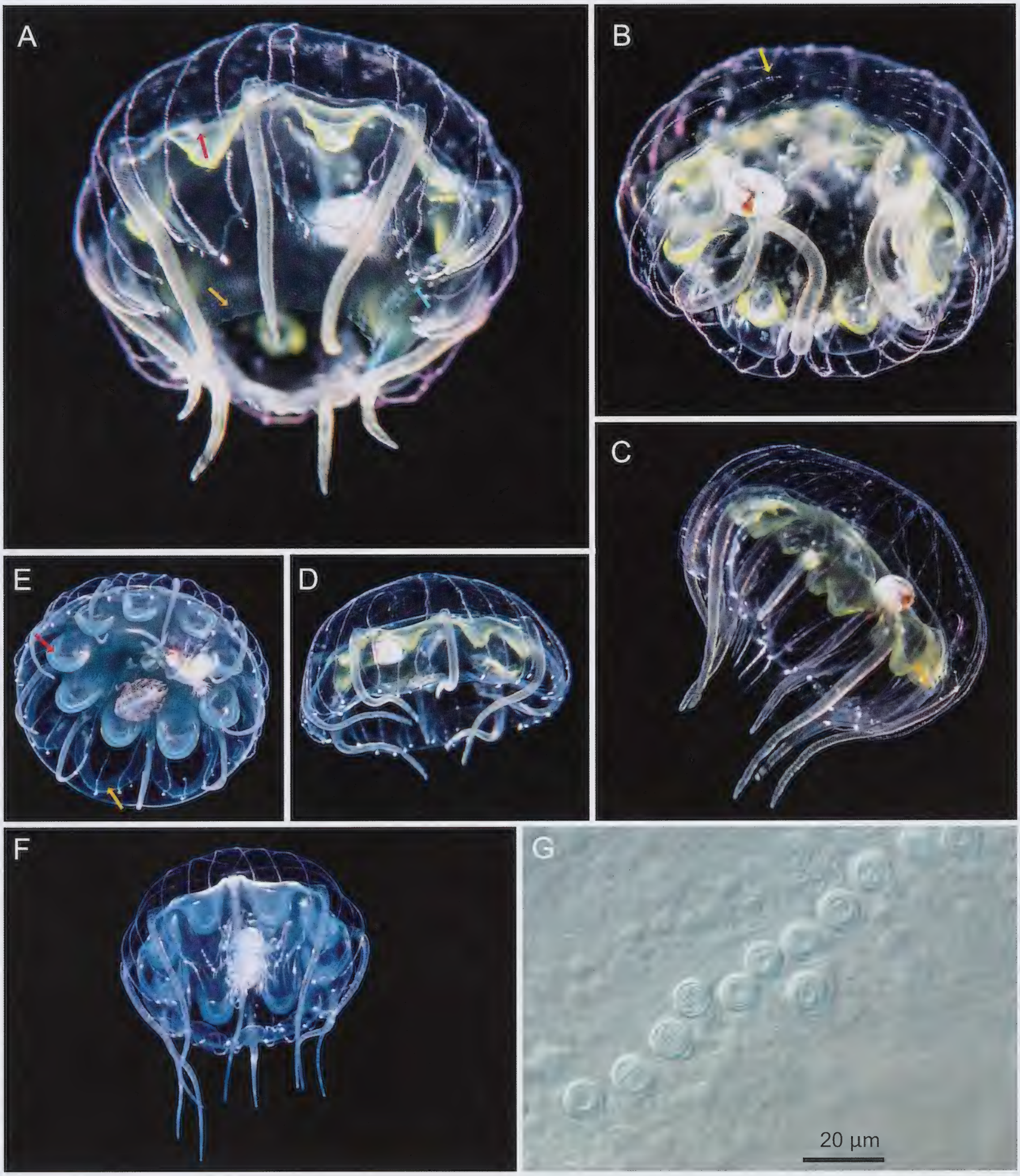


Fig. 54. *Pegantha polystriata*. (A-D) BFLA4450, bell diameter 5 mm. (A) Oblique view from oral side, the blue arrow points to a statocyst, the yellow one to the velum, the red one to the outer margin of the stomach. (B) Oblique view on bell top, arrow indicates otoporpae reaching almost to top of bell. (C-D) Lateral views, the arrow indicates the outer margin of the stomach. (E-F) Photos taken by Linda Ianniello, reproduced with the kind permission of the author. (E) Animal observed 21-Mar-2020 with nine tentacles, yellow arrow indicates peripheral canals, red arrow a gonad diverticulum hanging into subumbrella. (F) Animal observed 15-SEP-2020, the gonad diverticula appear like manubrial pocket. (G) BFLA4450, alcohol preserved, isorhiza nematocysts from exumbrellar otoporpae.

otoporpae sometimes irregular, branching, or not straight. Exumbrella apart of the nematocyst tracks smooth, without radiating keels or furrows. Velum broad (Fig. 54A). Stomach large, circular; near its periphery and positioned interradially 8 to 9 diverticula for the gonads (Fig. 54A-F), originating from stomach floor, in younger animals shallow, in older ones hanging into subumbrella (Fig. 54E); diverticula with thickened walls, dense tissue, sometimes yellow-green tint. Lappets of bell margin apparently with broad peripheral canal, difficult to see and observed only in one animal (Fig. 54E). Eight or nine thick, tapering tentacles originating in about middle of bell height in the bays between adjacent lappets (peronia), tentacles continued at right angles into the jelly as a pointed tentacle-root, tentacles held mostly in oral direction. Statocysts pendant, club shaped, with 2 to 5, usually 3, statoliths in a row, these increasing in size distally. Exumbrellar nematocysts: spherical isorhizas, ca. 10 *µm* (Fig. 54G).

16S data: The single sequence obtained clustered in a clade comprising other *Pegantha* as well as *Cunina* and *Pseudaegina* species, but without resolved internal relationships (Fig. 48).

Distribution: South China Sea, Taiwan Strait (Xu *et al*., 2014), Florida (this study). Type locality: Southern end of Taiwan Strait, 22.5°N, 118.5°E.

Remarks: Our medusae, especially the younger ones (Fig. 54C-D), appear indistinguishable from figures of *Otoporpa polystriata* given in Xu & Zhang (1978) and we are convinced that they are the same, despite this species is so far only known from the South China Sea. However, we think that this species was not classified in the correct family. The genus *Otoporpa* Xu & Zhang, 1978 was originally placed in the family Aeginidae (*sensu* Bouillon *et al.*, 2006) because it had apparently interradial manubrial pouches. The pouches of *Otoporpa* are atypical for Aeginidae as they are rather shallow and most importantly they are not sub-divided by a medium septum (see Fig. 51C, G). Likewise unusual for genera of the former Aeginidae (*sensu* Bouillon *et al.*, 2006), *Otoporpa* has otoporpae (thickenings clasping the bell margin and usually continued as nematocyst tracks on the exumbrella, comp. Figs 50C-D, 53B, D). We think that Xu & Zhang (1978) misinterpreted the developing gonad diverticula typical of the genus *Pegantha* as manubrial pouches. This is understandable as younger stages of these diverticula resemble indeed interradial manubrial pouches (Fig. 54C-D, F).

It is possible that some of the Brazilian specimens described by Tosetto *et al.* (2018) as *Pegantha triloba* Haeckel, 1879 belong to the present species. Tosetto's material lacked the diagnostic radial exumbrellar keels and furrows as shown in Bigelow (1909), it had 8 to 9 lappets and tentacles instead of 12 to 16 (Kramp, 1959a), and the otoporpae continued as nematocyst tracks to almost the top of the umbrella. The otoporpae in *P. triloba* are usually much shorter, but Kramp (1957) found also very long ones like in the present species in young *P. triloba*.

Genus *Solmaris* Haeckel, 1879

Pachysoma Kölliker, 1853: 322, type species *Pachysoma flavescens* Kölliker, 1853 by monotypy; invalid junior homonym of *Pachysoma* Macleay, 1821 [Insecta].
Solmaris Haeckel, 1879: 355, type species *Aequorea rhodoloma* Brandt, 1838 (designation by Kramp, 1961).
Solmaris (*Solmarium*) Haeckel, 1879: 355.
Solmaris (*Solmarinus*) Haeckel, 1879: 357.

Diagnosis: Narcomedusae without manubrial pouches; without peripheral canal system; mostly simple annular gonads on manubrial wall; with numerous tentacles leaving exumbrella at the level of manubrium attachment to subumbrella. Without otoporpae.

Remarks: For a synopsis of species in this genus see Bouillon *et al.* (1991: 408).

Solmaris corona (Keferstein & Ehlers, 1861)

Fig. 55A-C

Aegineta corona Keferstein & Ehlers, 1861: 94, pl. 14, figs 7-9.
Solmaris (Solmarinus) coronantha Haeckel, 1879: 359, pl. 20 figs 7-10, Canary Islands.
? *Solmaris multilobata* Maas, 1893: 45, pl. 4 figs 1-5.
Solmaris corona. – Haeckel, 1879: 358. – Mayer, 1910: 437, figs 288-289. – Russell, 1953: 476, figs 313, pl. 28 fig. 2. – Kramp, 1961: 278. – Pages, Gili, Bouillon, 1992: 42, fig. 51. – Bouillon *et al*., 2004: 236, fig. 147. – Nagata *et al.,* 2014: 313, fig. 33.

Examined material: BFLA3837; 1 specimen; 19-NOV-2018; size approximately 2-3 mm, 18 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528660. – BFLA4123; 1 specimen; 06-JUN-2019; size 9 mm, 25 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528679. – BFLA4314; 1 specimen; 24-JAN-2020; size 2 mm, 15 tentacles; preserved in alcohol for DNA extraction; 16S sequence MW528706. – 31-AUG-2018; 1 specimen photographed, 18 tentacles, not collected.

Observations: Umbrella diameter up to 9 mm, jelly lenticular (Fig. 55A), top with a broad, shallow apical projection; periphery with up to 25 lappets, distinctly rectangular (Fig. 55A-C), 1-3 statocysts per lappet (Fig. 55A). Stomach large, more than 2/3 of bell diameter, without gastric pockets, no peripheral canals. Presumable gonad tissue developing as slightly opaque ring on oral side of stomach (Fig. 55A). Up to 25 tentacles, issuing in about middle of bell height, curving upwards, rather stiff, but able to move and even to coil,

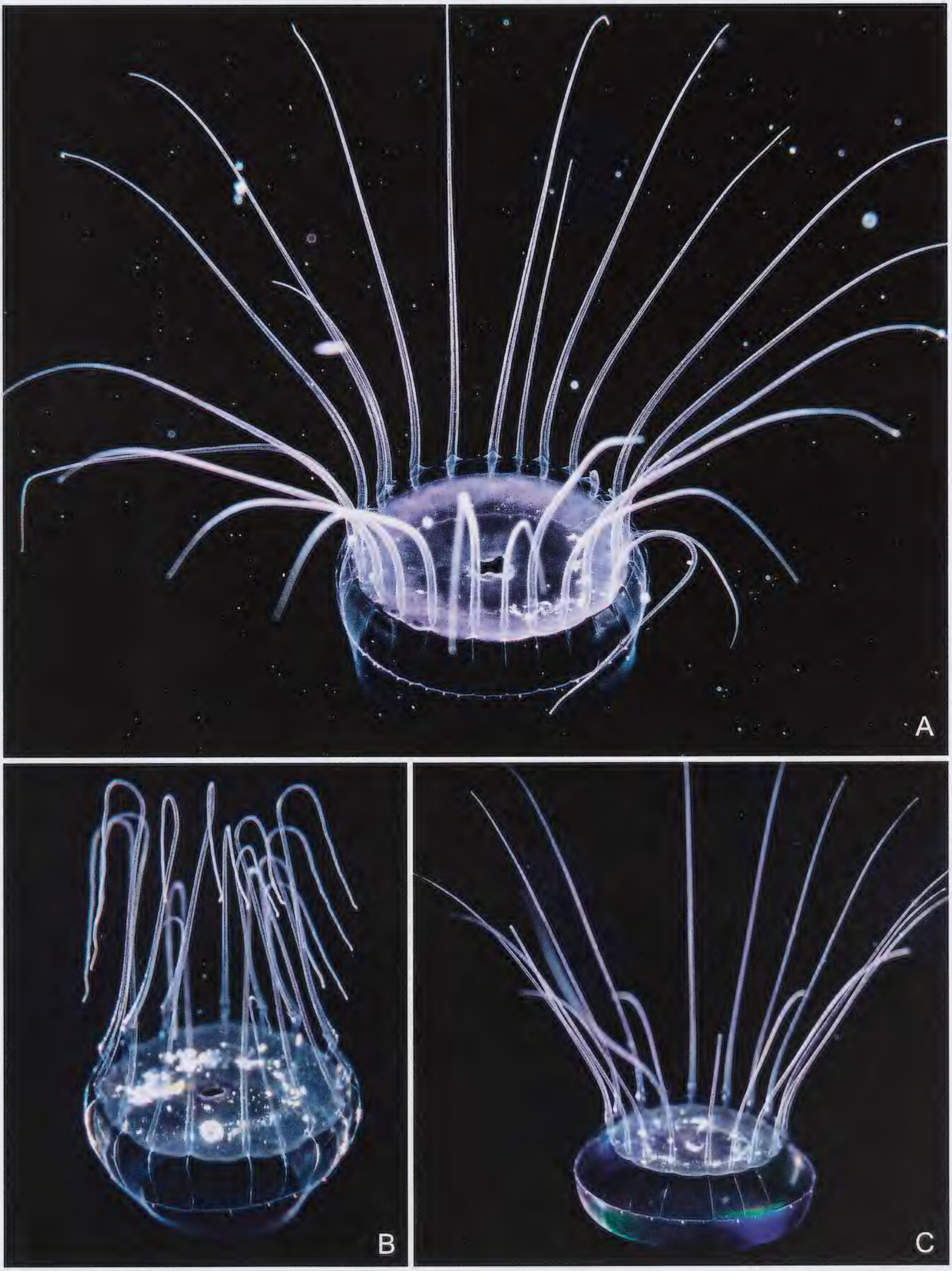


Fig. 55. *Solmaris corona*. (A) Specimen BFLA4123, diameter 9 mm. (B) BFLA4314, diameter 2 mm. (C) BFLA3837, diameter 2-3 mm.

evenly tapering to tip, length about 2-3 bell diameters, root short. Below tentacles no exumbrellar furrows, but thin peronia delimiting the lappets. Colour: stomach and tentacles a purple hue (Fig. 55A), some tentacle tips a very faint yellow (Fig. 55B).

16S Data: See Table 1 and Fig. 48.

Distribution: In the eastern Atlantic, from Norway to South Africa, in the western Atlantic from Florida to Brazil, also Indian Ocean (South Africa) (Pagès *et al.*, 1992; Nagata *et al.,* 2014; this study). Type locality: Mediterranean, Bay of Naples.

Remarks: Our identification as *S. corona* was primarily based on the description given in Russell (1953) and Pages *et al.* (1992). It is somewhat tentative because our specimens were probably not fully grown as they did not attain the maximal tentacle number of 36 and size of 12-15 mm given in Kramp (1953). The observed maximal number of 25 tentacles compares more favourably with the numbers given in the original description for mature animals (27-30, 14 mm diameter; Keferstein & Ehlers, 1861). Russell (1953) provides a table with observed sizes and tentacle numbers for an Irish population and our specimens agree approximately. During the course of its development *S. corona* changes very little in general appearance. There is merely an increase in the number of marginal lappets, tentacles, and sense organs (Russell, 1953).
It was not clear if the opaque ring in the stomach (Fig. 55A) is the developing gonad tissue or some residual, digested food. The slight purple colour let us favour it being the developing gonad tissue.

Solmaris flavofinis n. spec.
Fig. 56A-H

Holotype: BFLA4068, 10-APR-2019; size 9 mm, mature female, 9 tentacles; part preserved in formalin and deposited as UF-013779 (damaged), small part preserved in alcohol for DNA extraction (MHNG-INVE-0137376); 16S sequence MW528665.

Paratype: BFLA4273; 04-DEC-2019; size 9 mm, 8 tentacles; preserved in formalin and deposited as UF-013841.

Other material: BFLA4243; 1 specimen; 11-NOV-2019; size 9 mm, 11 tentacles; preserved in alcohol for DNA extraction; 16S sequence identical to MW528665. – BFLA4250; 1 specimen; 23-NOV-2019; size 8 mm, 10 tentacles, mature female; preserved in alcohol for DNA extraction; 16S sequence MW528693.

Etymology: The specific epithet is derived from the Latin words *flavus* (yellow) and *finis* (end), an allusion to the yellow tentacle tips.

Description: Bell diameter 8-9 mm, height ~4-5 mm, lower part shaped somewhat conical, upper part less steep, with small, rounded apical projection (Fig. 56C); lower third of bell composed of 8 to 11 rectangular lappets (Fig. 56A-F), 1-2 statocysts per lappet (Fig. 56E). Stomach large, 2/3 of bell diameter, flat, without gastric pockets, no peripheral canals. Gonad tissue developing on periphery of oral side of stomach (Fig. 56A, B, F), only females unambiguously identified, forming up to 8 very large oocytes (Fig. 56B), often but not always in perradial position, size estimate ~0.7 mm, flattened lentil-shaped, well visible germinal vesicle (nucleus). 8 to 11 thin tentacles, issuing in about 1/3 of bell height, held upward (Fig. 56C) or downward (Fig. 56A), rather stiff, but able to move and even to coil (Fig. 56F), evenly tapering to tip, length about two bell diameters, root short (Fig. 56G). Below tentacles no exumbrellar furrows, but thin peronia delimiting the lappets. Statocysts bipartite, with inverted cone as base and spherical end with statocysts (Fig. 56H). Colour: colourless except for yellow tentacle tips (Fig. 56A, D).

16S Data: See Table 1 and Fig. 48. The p-distance to *S. corona* was very high (32%).

Remarks: The combination of the traits tentacle number (9-11), size (8-9 mm), and shape of the marginal lobes did not fit any of the known and accepted *Solmaris* species listed in Bouillon *et al.* (1991). Both the 16S and the morphological traits varied only in a relatively narrow range and we are convinced that these medusae represent a distinct species. The species resembling *S. flavifinis* most closely is the Mediterranean *Solmaris flavescens* (Kölliker, 1853) (for a good description see Mayer, 1910: 434, figs 284-286). *Solmaris flavescens* differs in being considerably larger (diameter 15-23 mm) and has more tentacles (usually 13-15, exceptionally 12 or 17). While the yellow tentacle tips of *S. flavifinis* permitted distinguishing it immediately from the co-occurring *S. corona* (see above), this is not a diagnostic trait because it is shared with *S. flavescens* (Kölliker, 1853: 322; Gegenbaur, 1857: 264; Metchnikoff, 1886: 19[257]). Another trait shared with *S. flavescens* is the large size of the oocytes, but several other Narcomedusae also have such large eggs (see table 4 in Bouillon, 1987).

Family Solmundaeginidae Lindsay, Bentlage & Collins, 2017

Solmundinae Haeckel, 1879: 349.
Solmundaeginidae Lindsay, Bentlage & Collins, 2017 in Lindsay *et al.,* 2017: 504.

Diagnosis: Narcomedusae with manubrial pouches interradial, divided into two to four parts; gonads in these pouches; exumbrellar, primary tentacles between marginal lobes; without a peripheral canal system; with two or four primary tentacles leaving umbrella

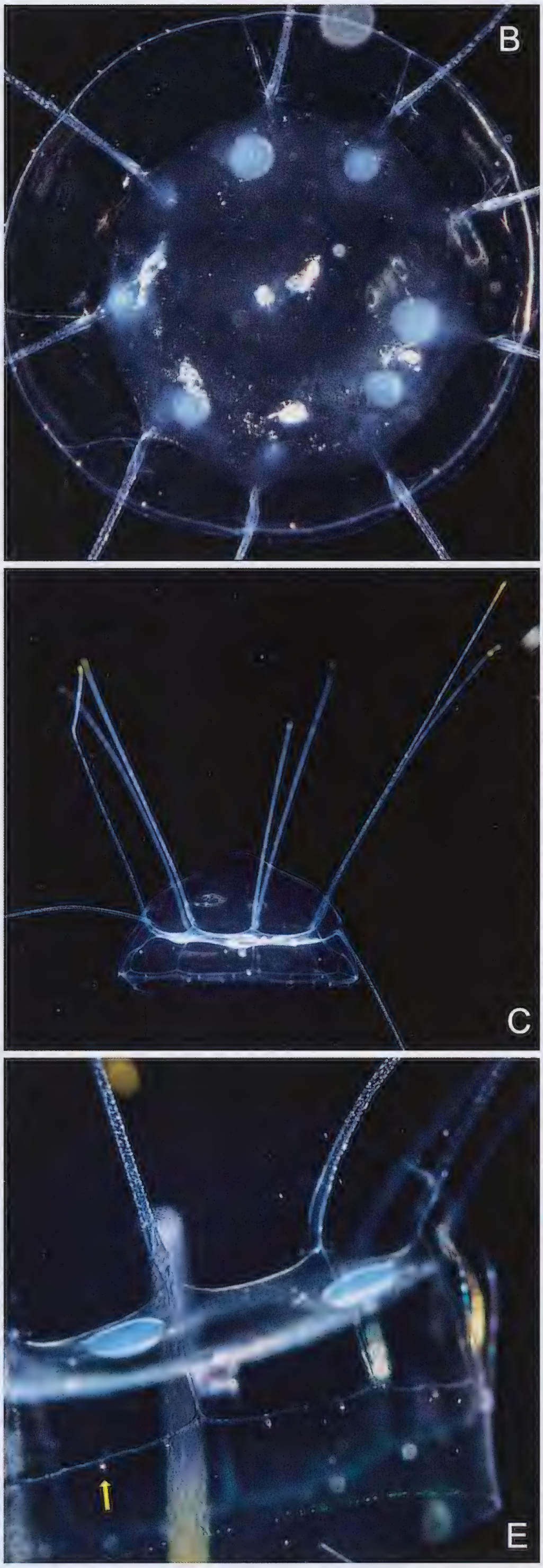


Fig. 56. *Solmaris flavofinis* n. spec. (A-C) Holotype (BFLA4068), diameter 9 mm. (A) Oblique view from aboral side. (B) View from aboral side, note large oocytes with germinal vesicles. (C) Lateral view. (D-F) BFLA4250, diameter 8 mm. (D) Lateral view. (E) Close up of three lappets with statocysts (arrow). (G) BFLA4243, 9 mm. (H) BFLA4273, preserved sample, statocyst enlarged.

in apical half, well above level of stomach pouches; tentacle roots acutely recurved orally; no nematocyst-laden, deep peronial grooves; with peronia, equal or twice as many in number as the primary tentacles; without secondary tentacles on umbrella margin but with rudimentary bulbs; with or without nematocyst patches covering exumbrella. Represented by the genera *Solmundaegina, Solmundella*, *Aeginopsis*, and *Solmundus* (Lindsay *et al*., 2017).

Remarks: When splitting the former Family Aeginidae, Lindsay *et al*. (2017) proposed this new family name based on their new genus *Solmundaegina* and included also the other genera listed above. They may have overlooked that by including the genus *Solmundus* Haeckel, 1879 there is already a family level name for this group available, namely the subfamily Solmundinae Haeckel, 1879, which is also valid at the family level as Solmundidae Haeckel, 1879. However, we agree with Lindsay *et al.* (2017) that the type species of *Solmundus* (*S. tetralinus* Haeckel, 1879) is a doubtful species, perhaps an aberrant *Solmundella bitentaculata* with four tentacles. Family names should not be based on dubious genera and species and it is advisable to remove *Solmundus* from the Solmundaeginidae.

Genus *Solmundella* Haeckel, 1879

Solmundella Haeckel, 1879: 352, type species *Charybdea bitentaculata* Quoy & Gaimard, 1833.

Aeginella Haeckel, 1879: 340, invalid junior homonym of *Aeginella* Boeck, 1861 [Crustacea].

Diagnosis: Narcomedusae with eight manubrial pouches; without peripheral canal system; four peronia, two long tentacles; no secondary tentacles; no otoporpae.

Solmundella bitentaculata (Quoy & Gaimard, 1833)

Fig. 57A-C

Carybdea bitentaculata Quoy & Gaimard, 1833: 295, pl. 25 figs 4-5.

Campanella capitulum Quoy & Gaimard in de Blainville, 1834: 286. – Agassiz, 1865: 169.

Aeginopsis mediterranea Müller, 1851: 277, pl. 11, Mediterranean.

Aeginella dissonema Haeckel, 1879: 340, pl. 20 fig. 16, Canary Islands. – Kramp, 1955b: 308, synonym.

Solmundella muelleri Haeckel, 1879: 352, Canary Islands. – Kramp, 1955b: 308, synonym.

Solmundella henseni Maas, 1893: 55, pl. 5 fig. 11, Florida Current.

Aeginella bitentaculata. – Haeckel, 1879: 341.

Solmundella bitentaculata. – Bigelow, 1909: 77, pl. 2 fig. 3. – Mayer, 1910: 455, fig. 301, record Florida. – Vanhöffen, 1912: 392. – Vanhöffen, 1913a: 428, record Florida. – Kramp, 1959a: 195, fig. 297. – Kramp, 1961: 270. – Rajan, 1963: 314, figs 1-5, larval stages. – Kramp, 1968: 124, fig. 338. – Goy, 1979: 285, fig. 26. – Segura-Puertas, 1984: 44, pl. 13 fig. 3. – Bouillon, 1987: 239, fig. 5, pl. 1 figs 1-5, development. – Pagès *et al.,* 1992: 38, fig. 43. – Buecher *et al*., 2005: 30. – Galea, 2007: 96, pl. 2O. – Wang *et al.,* 2014: 98, fig. 3

Solmundella bitentaculata var. *mediterranea*. – Mayer, 1910: 456, fig. 302, pl. 54 figs 1-3, pl. 55 fig. 4. – Neppi & Stiasny, 1913: 60.

Solmundella mediterranea. – Vanhöffen, 1912: 393, status. – Browne, 1916: 201. – Thiel, 1936: 68, synonym.

Examined material: BFLA4119; 1 specimen; 04-JUN-2019; size 4 mm; preserved in alcohol for DNA extraction; 16S sequence MW528677. – BFLA4422; 1 specimen; 28-MAY-2020; size 2 mm; preserved in alcohol for DNA extraction but specimen was lost. – 24-SEP-2018; 1 specimen; photographed, not collected. MHNG-INVE-31746; Mediterranean, Bay of Villefranche-sur-Mer; 43.6860°N 7.3170°E; 0-70 m depth; collection date 03-MAY-2001; 2 mature males, 4 mm diameter; part preserved in formalin, part in ethanol in alcohol for DNA extraction; 16S sequence KX355407. – 28-APR-2014; locality as previous sample; 1 specimen, 3 mm diameter, with gonads; preserved in alcohol for DNA extraction; 16S sequence MG811640.

Description: Florida specimens with bell size up to 4 mm, as wide as high, umbrella circumference round (not oval, Fig. 57C), apical jelly thick resembling an apical process (Fig. 57B), evenly rounded and not keeled or oval in transverse section. Stomach wide, up to 7/10 of bell diameter, lenticular, without distinct gastric jelly cone; eight rectangular stomach pouches, no peripheral canal visible. Two opposite tentacles, these thick and long (~18 mm), tapering, originating in middle of bell, held variably upward or downward, held upwards in furrow of exumbrella that reaches almost to top of umbrella, below tentacles also a furrow with peronium, intertentacular peronium indistinct. Bases (roots) of tentacles in mesoglea, tapering, curved towards oral. 14 or more statocysts. Mouth region green, tentacles sometimes with broad yellow regions.

16S Data: See Table 1 and Fig. 48. The available 16S sequences appear polyphyletic, notably the one from an Antarctic medusa is clearly not related to the other ones which all form a well supported clade, but with deep subdivisions.

Distribution: Widely distributed in all oceans, including the Mediterranean, but rare in the northern parts of the Atlantic and Pacific Oceans; circumpolar in Antarctic seas; from surface to fairly deep water (Kramp, 1959a). This species is one of the most widespread of planktonic animals and is found at nearly all latitudes (Larson & Harbison, 1990). Type locality: Pacific Ocean, Banda Sea, Bay of Ambon (Moluccas, Indonesia).

Remarks: The taxonomic history of *Solmundella bitentaculata* is marked by the question whether

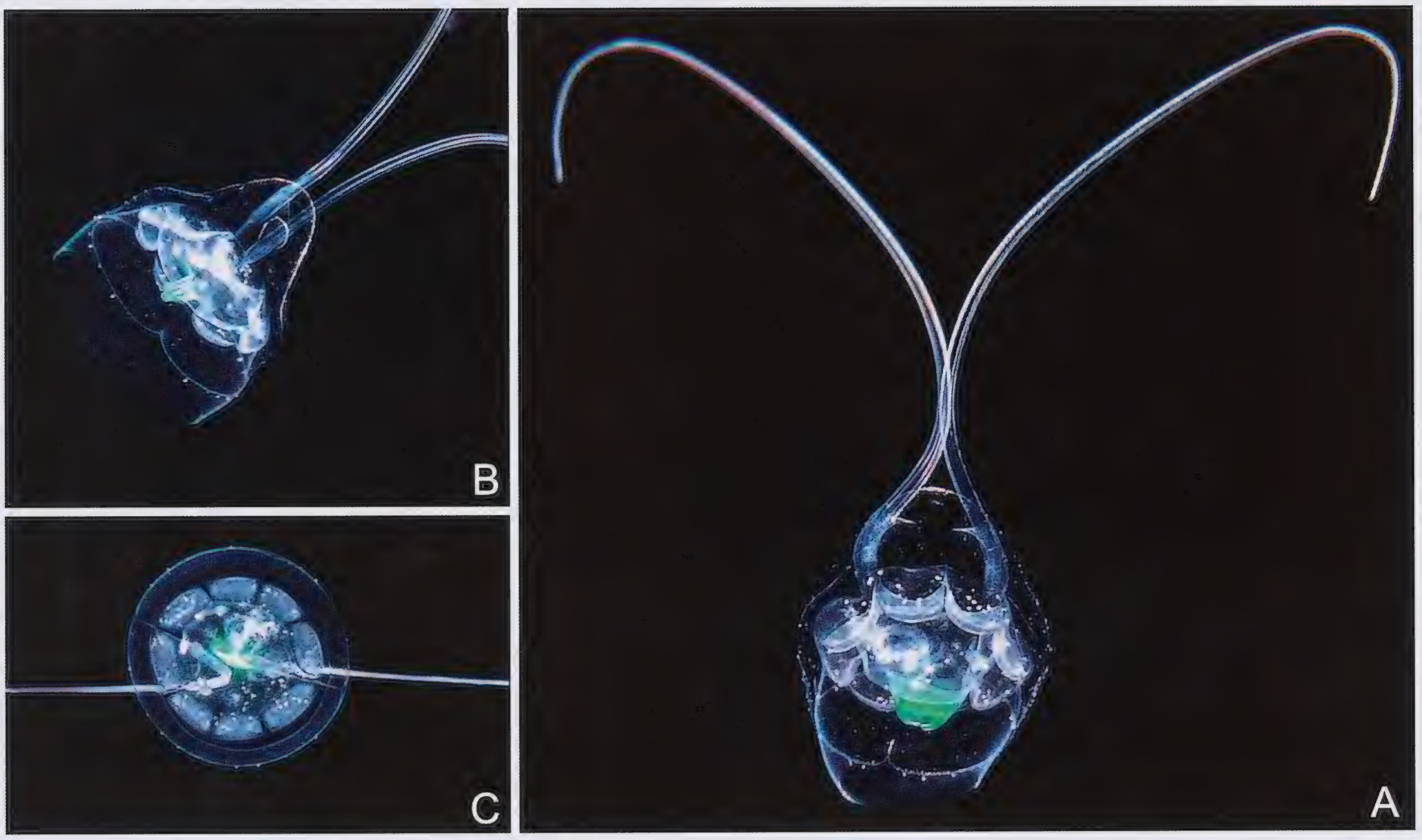


Fig. 57. *Solmundella bitentaculata*, sample BFLA4119, bell diameter 4 mm. (A-B) Lateral views of whole animal, note the green mouth region. (C) Aboral view.

S. mediterranea is distinct from it or conspecific. Summarizing Mayer (1910) and Browne (1916), the two differ by the following traits [in square brackets traits observed in the present study]:

- size when fully mature (12-15 mm *versus* 4-6 mm) [4 mm]
- shape (bell outline, diameter in tentacular axis larger than in intertentacular axis, bell apex keel-shaped *versus* circular bell and apex rounded)[round]
- tentacle length (up to 100 mm versus 10-18 mm) [18]
- peronial furrows (perradial ones deep versus all shallow)[shallow]
- statocysts in fully grown animals (16 versus 8) [14]

Mayer (1910) and Browne (1916) thought that the two names refer to simple variants or growth stages. Thiel (1936) and Kramp (1955b; 1961) listed them as synonyms, this being accepted by subsequent authors. Our Florida specimens matched mostly the *S. mediterranea* morphotype, except for the statocyst number.

Another geographic variation was reported by Vanhöffen (1912) and Browne (1916) for Antarctic populations: they have clusters of nematocysts on the ex-umbrella, especially near the margin.

The maximum likelihood tree (Fig. 48) shows that one sequence (EU293998, from Antarctica according to voucher specimen data) is far apart from the other *Solmundella* which cluster in a monophyletic clade. However, there are possibly some problems with the identification of this specimen as it has almost the same sequence as an *Aegina citrea* of unknown origin (KY007598). The 16S of the Pacific, Mediterranean, and Gulf stream samples formed a well supported clade. The divergences within this clade are high (Table 1) and the three subclades could represent three species. A reconsideration of the morphological differences and the different nominal species in the synonymy listed above is thus warranted. Unfortunately, no morphological data are available for the Pacific specimens used to get the 16S sequences.

Order Trachymedusae
Family Rhopalonematidae Russell, 1953
Genus *Aglaura* Péron & Lesueur, 1810

Aglaura Péron & Lesueur, 1810: 351; type species *Aglaura hemistoma* Péron & Lesueur, 1810 by monotypy.

Lessonia Eydoux & Soulyet, 1852: 643; type species *Lessonia radiata* Eydoux and Soulyet, 1852 by monotypy; preoccupied by *Lessonia* Swainson, 1832 [Aves].

Stauraglaura Haeckel, 1879: 277; type species *Stauraglaura tetragonima* Haeckel, 1879 by monotypy; nomen dubium.

Diagnosis: Rhopalonematidae with slender gastric peduncle; with eight mobile, sausage-shaped gonads attached on peduncle and not on subumbrella; tentacles numerous, all alike; with pendant, club-shaped statocysts on bell margin.

Aglaura hemistoma Péron & Lesueur, 1810
Fig. 58A-D

Aglaura hemistoma Péron & Lesueur, 1810: 351. – Haeckel, 1879: 275, pl. 16 figs 3-4. – Vanhöffen, 1902: 78, synonymy. – Bigelow, 1909: 119, pl. 2 fig. 6, synonymy. – Mayer, 1910: 398, fig. 254, pl. 46 figs 4-5, pl. 49 figs 3-7, pl. 50 fig. 11. – Kramp, 1959a: 192, fig. 291 – Kramp, 1961: 251. – Kramp, 1965: 127, distribution. – Kramp, 1968: 122, fig. 331. – Bouillon, 1978a: 162, cnidome. – Fagetti, 1973: 41, pl. 4 fig. 13. – Goy, 1979: 284, fig. 25. – Pagès *et al*., 1992: 44, fig. 53. – Bouillon *et al*., 2004: 241, fig. 152G. – Nagata *et al*., 2014: 316, figs 36-37.

Lessonia radiata Eydoux & Soulyet, 1852: 643, pl. 2 fig. 16, Pacific Ocean.

Aglaura Peronii Leuckart, 1856: 10, pl. 1 fig. 5, Mediterranean. – Haeckel, 1879: 275, synonym.

Aglantha globuligera Haeckel, 1879: 272, pl. 16 fig. 8, Canary Islands. – Kramp, 1959a: 192, synonym.

Aglaura nausicaa Haeckel, 1879: 274, pl. 16 fig. 1, Mediterranean.

Aglaura laterna Haeckel, 1879: 274, pl. 16 fig. 2, Canary Islands.

Stauraglaura tetragonima Haeckel, 1879: 277, pl. 16 figs 10-11, coast of Australia. – Kramp, 1961: 264, probably *A. hemistoma*.

Aglaura prismatica Maas, 1897: 24, pl. 2 figs 4-5, Gulf of Panama, Pacific Ocean. – Maas, 1906a: 97, pl. 3 fig. 12.

Aglantha octogona Bigelow, 1904: 257, pl. 7 fig. 9, Maldives.

Aglaura ciliata Perkins, 1906: 118, Tortugas.

Examined material: BFLA3808; 4 specimens observed, one collected; 19-OCT-2018; size 2 mm; preserved in alcohol for DNA extraction; 16S sequence MW528640. – BFLA4214; 1 specimen; 27-AUG-2019; 2 mm; parts preserved in formalin (UF-013830) and in alcohol for DNA extraction; 16S sequence MW528686. – 20-AUG-2019; 1 specimen photographed; size 3 mm; not collected.
MHNG-INVE-0031745; Mediterranean, Bay of Villefranche-sur-Mer, 43.6860°N 7.3170°E, depth 0-70 m; collection date 03-MAY-2001; numerous specimens collected, some preserved in formalin, one used for DNA extraction, 16S sequence KP776748.

Observations: Specimens from Florida with bell size of 2 mm, cylindrical shape, aboral side with funnel-like depression (Fig. 58C), wall very thin, velum broad, with slender gastric peduncle of 2/3 of subumbrellar height (Fig. 58D). Manubrium protruding through velar opening (Fig. 58A-D), bipartite, upper part sac-like, lower half with cruciform cross-section, ending in four-lipped mouth (Fig. 58B), margins smooth, not crenulated. Gonads eight sausage-shaped apendices in a whorl attached at junction of manubrium to peduncle (Fig. 58A-C). Eight radial canals, thin and very transparent. Seven or eight statocysts (Fig. 58B) on bell margin and about 70 thin tentacles. Mostly colourless, but interference effects often cause iridescence in rainbow colours (Fig. 58A, D).

16S Data: The two haplotypes of this study differed in 0.9% of the base pairs, while the minimal differences to other population were 2 to 5 % (Table 1). In a maximum likelihood tree (not shown) obtained by comparing it to the Trachymedusa 16S dataset of Bentlage *et al*. (2018) and additional trachyline sequences from GenBank, all *Aglaura hemistoma* clustered as a monophyletic group.

Distribution: Widely distributed and common in the warm and temperate parts of the Atlantic-, Indian-, and Pacific Oceans, usually between about 40°N and 40°S including also the Mediterranean, usually in large numbers (Kramp, 1965; Fagetti, 1973; Bouillon, 1978b; Goy, 1979; Navas-Pereira &Vannuci, 1991; Pagès *et al.,* 1992; Nagata *et al.,* 2014). Type locality: Mediterranean Sea, near the town of Nice.

Remarks: Although *Aglaura hemistoma* has numerous synonyms, it is taxonomically rather unproblematic. Providing a tabular comparison of the nominal *Aglaura* species, Vanhöffen (1902) concluded that they are mostly developmental stages or variants of *A. hemistoma*. Moreover, *A. hemistoma* has a very thin jelly which gets deformed quite drastically when preserved (Bigelow, 1909). Our own observations on material from the Mediterranean showed that the bell actually elongates considerably in formalin. Some authors may have misinterpreted this fixation effect as a diagnostic trait and it explains the number of synonyms. The few available 16S sequences are also relatively similar (Table 1).

Genus *Amphogona* Browne, 1905

Amphogona Browne, 1905: 739, type species *Pantachogon apsteini* Vanhöffen, 1902 by monotypy.

Diagnosis: Rhopalonematidae with short, thin gastric peduncle, exumbrella without apical process; eight ellipsoidal or sac-shaped, pendant gonads on radial canals; tentacles thin, all alike, without permanent terminal swelling; statocysts free, club-shaped.

Amphogona apsteini (Vanhöffen, 1902)
Fig. 59A-B

Pantachogon apsteini Vanhöffen, 1902: 65, pl. 10 fig. 18, pl. 11 fig. 28.

Amphogona apsteini. – Browne, 1905: 740, pl. 54 fig. 5, pl. 56 fig. 1, pl. 57 figs 10-15. – Bigelow, 1909: 126, pl. 2 figs 1-2, pl. 34 figs 12-15, pl. 45 fig. 10. – Mayer, 1910: 405, fig. 257. – Kramp, 1959a: 188, fig. 280. – Kramp, 1965: 123, figs 12-13. – Kramp, 1968: 118, fig. 319. – Bleeker & Van der Spoel, 1988: 241, fig. 37.

Examined material: BFLA; 1 specimen; 09-DEC-2019; size 2 mm, juvenile; preserved in alcohol for DNA extraction; 16S sequence could not be obtained as PCR failed repeatedly. – 05-JUL-2019; 2 specimens photographed, 2 mm, not collected.

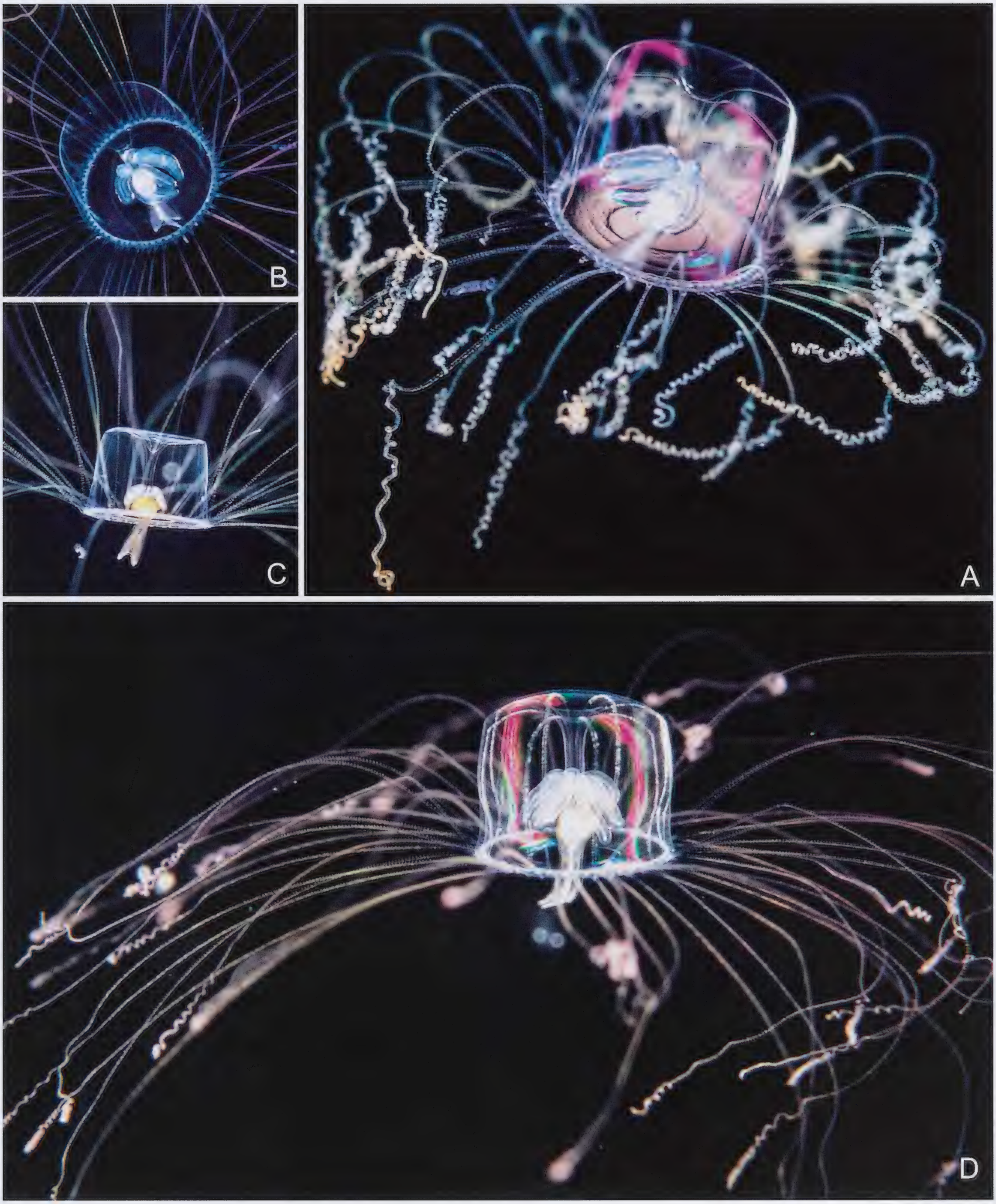


Fig. 58. *Aglaura hemistoma*. (A-B) Sample BFLA3808, bell size 2 mm, oblique views from oral side. The statocysts can be seen in B as tiny, bright spots along the ball margin. (C) Animal photographed 20-AUG-2018, bell size 3 mm. (D) BFLA4214, bell size 2 mm, lateral view.

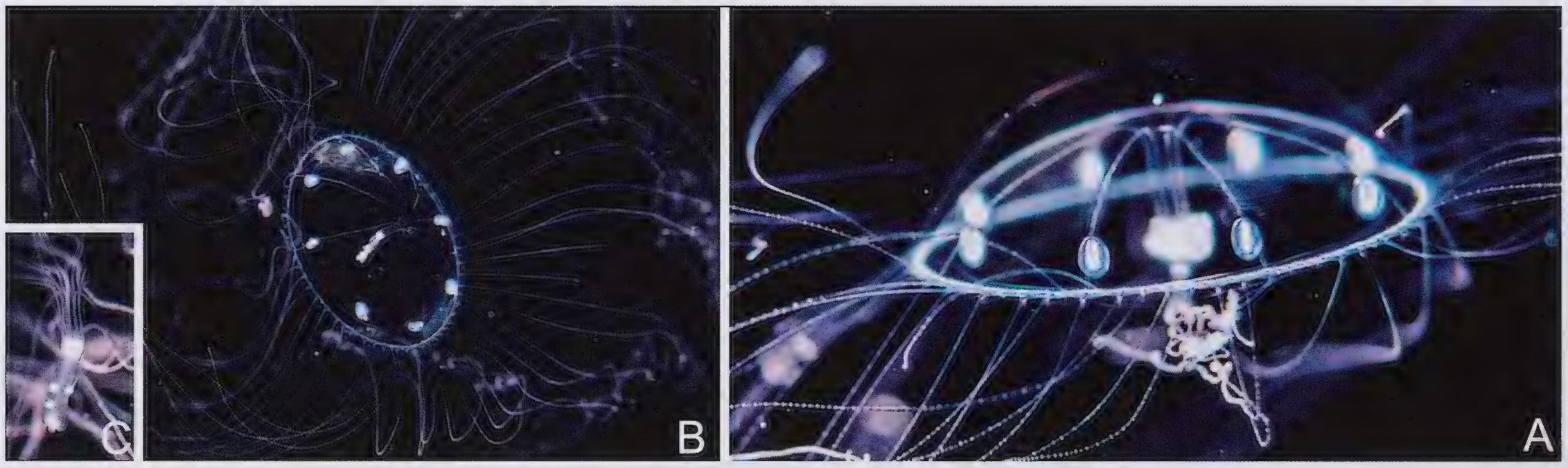


Fig. 59. *Amphogona apsteini*, bell size 2 mm, 09-DEC-2019. (A-B) Two separate individuals. (C) Close up of manubrium and gastric peduncle.

Observations: Bell diameter 2 mm, flatter than hemisphere, jelly relatively thin especially towards margin; with thin gastric peduncle reaching almost to level of velum (Fig. 59B); stomach small, lips inconspicuous. Eight radial canals. Gonads when fully developed ellipsoidal, pendant, close to ring canal, all of equal size or larger ones and smaller ones alternating; long axis of ellipsoidal gonads vertical (Fig. 59A). About 70 tentacles, all the same structure. One to two statocysts per octant.

Distribution: Circumglobal in warm waters. In the Indian Ocean from Indonesia to Moçambique (Kramp, 1953, 1968; Bouillon, 1978a); in the Pacific Ocean from eastern Australia, to the northern Part of the China Sea and Peru (Kramp, 1953, 1965; Bouillon, 1978c; Du *et al*., 2010; Oliveira *et al.,* 2016). In the South Atlantic from Argentina to Brazil and to western Africa (Kramp, 1955b; Nagata *et al*., 2014; Oliveira *et al.*, 2016). In the North Atlantic reported from the mid Atlantic to Florida (Bleeker & Van der Spoel, 1988; Larson *et al.*, 1991; this study). Type locality: Indian Ocean, west coast of Sumatra.

Remarks: Kramp (1959a, 1965, 1968) states that the unequal size of the gonads, with small and larger ones alternating, is a characteristic trait of this species. However, this is found only in younger specimens, mature ones seem to have equally developed gonads (Bigelow, 1909; Nagata *et al.,* 2014). Kramp gives also a bell size of 4 to 6 mm. Our specimens were smaller (2 mm). The type material was 2 to 3 mm in size, although perhaps not fully mature. Also Nagata *et al.* (2014) give a bell size of 2 to 3 mm.

Genus *Rhopalonema* Gegenbaur, 1857

Trachynema Gegenbaur, 1854: 53; type species *Trachynema ciliatum* Gegenbaur, 1854 by monotypy.

Rhopalonema Gegenbaur, 1857: 251; type species *Rhopalonema velatum* Gegenbaur, 1857 by monotypy.

Calyptra Leuckart, 1856: 14; type species *Calyptra umbilicata* Leuckart, 1856 by monotypy; invalid junior homonym of *Calyptra* Ochsenheimer 1816 [Lepidoptera] and others.

Marmanema Haeckel, 1879: 261; type species not designated.

Trachyneme Whiteaves, 1901: 29; spelling error.

Diagnosis: Rhopalonematidae without gastric peduncle; gonads along radial canals; marginal tentacles solid, of two kinds: perradial tentacles long, with large, club-shaped ending; inter- and adradial tentacles short with swollen end. Statocysts enclosed in mesoglea when fully developed.

Rhopalonema velatum Gegenbaur, 1857

Fig. 60A-E

? *Trachynema ciliatum* Gegenbaur, 1854: 53, pl. 2 figs 17-23. – Gegenbaur, 1857: 259, pl. 9 fig. 6.

? *Calyptra umbilicata* Leuckart, 1856: 14, pl. 1 figs 9-10. – Mayer, 1910: 378, possibly *R. velatum*.

Rhopalonema velatum Gegenbaur, 1857: 251, pl. 9 figs 1-5. – Bigelow, 1909: 129, pl. 2 fig. 8, pl. 45 fig. 11. – Mayer, 1910: 378, figs 213-222, 224, synonymy. – Russell, 1953: 430, figs 283-284, synonymy. – Kramp, 1959a: 185, fig. 270. – Kramp, 1961: 262. – Kramp, 1968: 114, fig. 307. – Horridge, 1969: 345, figs 3-4, statocysts. – Segura-Puertas, 1984: 38, pl. 10 fig. 4. – Bleeker & Van der Spoel, 1988: 239, fig. 28. – Pagès *et al.,* 1992: 45, fig. 55.

? *Sminthea leptogaster* Gegenbaur, 1857: 246, pl. 9 fig. 11, Mediterranean. – Mayer, 1910: 383, possible synonym.

Trachynema octonarium Haeckel, 1879: 260, Canary Islands. – Mayer, 1910: 378, synonym.

Marmanema tympanum Haeckel, 1879: 262, Mediterranean. – Mayer, 1910: 378, synonym.

Marmanema clavigerum Haeckel, 1879: 263, pl. 17 figs 1-2, Canary Islands. – Kramp, 1961: 262, synonym.

Rhopalonema coerulum Haeckel, 1879: 264, pl. 17 figs 3-6, Canary Islands. – Kramp, 1961: 262, synonym.

Rhopalonema polydactylum Haeckel, 1879: 265, pl. 17 figs 7-1, Mediterranean. – Kramp, 1961: 262, synonym.

Marmanema velatoides Maas, 1893: 13, pl. 1 fig. 6, Atlantic. – Mayer, 1910: 378, synonym.

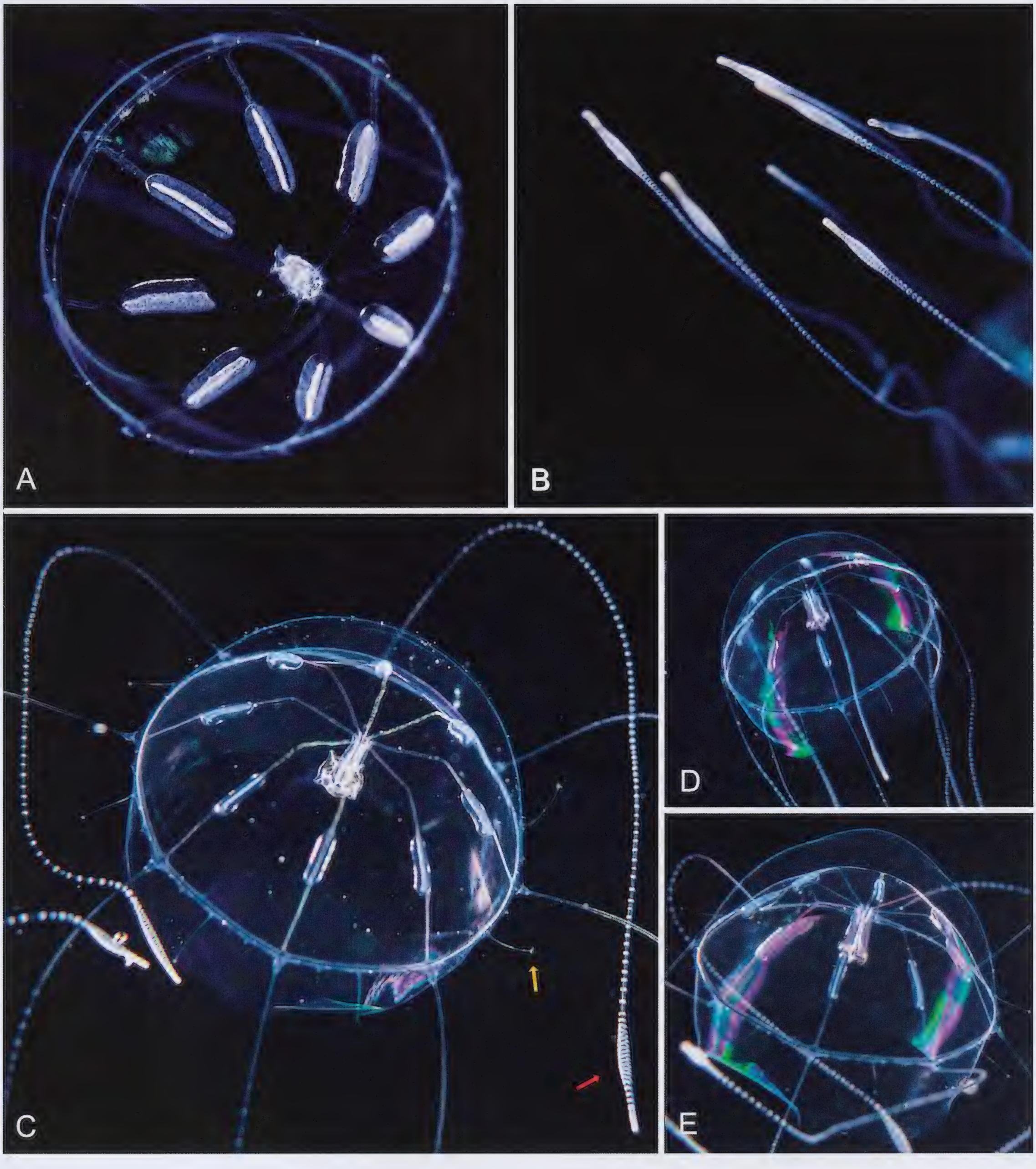


Fig. 60. *Rhopalonema velatum*. (A-B) Specimen of 04-MAR-2019, diameter ca. 11 mm. (A) Oblique view from aboral side. (B) Tentacle tips. (C-E) BFLA4292, 7 mm diameter. (C) Oblique view from aboral side, yellow arrow points to short, interradial tentacle, red arrow points to long, perradial tentacle. (D) Oblique view from oral side. (E) Near lateral view, note the slight apical process.

Rhopalonema striatum Maas, 1893: 15, pl. 1 figs 3-4, Atlantic.
– Kramp, 1961: 262, synonym.

Examined material: BFLA4289; 1 specimen; 09-DEC-2019; size 8 mm; no photos taken, preserved in alcohol for DNA extraction; 16S sequence MW528700. – BFLA4292; 1 specimen; 09-DEC-2019; size 7 mm; preserved in alcohol for DNA extraction; 16S sequence MW528702. – 04-MAR-2019; 1 specimen; size 11 mm, photographed, not collected.

Mediterranean, France, Bay of Villefranche-sur-Mer,

43.6860°N 7.3170°E, depth 0-70 m; 3 specimens collected 09-MAY-2001, 04-APR-2005, 29-APR-2014, used for DNA extractions, 16S EU293992 and KP776749.

Observations: Specimens from Florida with bell size of 7-11 mm, bell flatter than hemisphere, at least in some a very shallow apical process visible (Fig. 60E). Velum very broad and hanging down like a curtain. Manubrium small, shorter than bell cavity height. Eight thin radial canals. Gonads on radial canals, elongated ovals, about 1/3 as long as the radial canal, placed in middle of the radial canals. About 16 statocysts, positioned closer to tentacles and not in middle of spaces between tentacles. Eight long, extensible tentacles ending in club-shaped swellings (Fig. 60B, C); eight short, thin tentacles in interradial position, with terminal swelling (Fig. 60B); up to two tentacle stumps in adradial position per octant (Fig. 60C, not well visible).

16S data: The two halplotypes found in the Florida material differ only in one base pair position and likewise also from a Mediterranean haplotype (Table 1). A further haplotype from Tierra del Fuego is more divergent (Table 1).

Distribution: Abundant in the warm and temperate waters of Atlantic, Indian, and Pacific oceans, including also the Mediterranean. Type locality: Mediterranean.

Remarks: The medusa from Florida was identified as *R. velatum* although it differed somewhat from typical specimens as described in Kramp (1959a). There are currently two accepted species in the genus *Rhopalonema*: *R. velatum* and *R. funerarium* Vanhöffen, 1902. *Rhopalonema velatum* differs from the former in having a small apical process, marked off from the rest of the umbrella by a transverse circular furrow or depression. The process varies considerably in size and form (Russell, 1953). *Rhopalonema funerarium* lacks this proces, has long gonads on the distal 2/3 of the radial canals, a very short manubrium, and 32 statocysts. In one of the sample photos (Fig. 60E), a shallow apical process is present. Additionally, the size and position of the gonads and the statocyst number and position matched more *R. velatum*, but the short manubrium was more like in *R. funerarium*. Although the latter species has been regarded as distinct by Kramp (1947, 1959a), others had doubts [see discussion and references in Russell (1953: 435) and Bouillon *et al.* (2004: 244)]. It could well be that *R. funerarium* is only an advanced growth stage of *R. velatum*.

Order Limnomedusae
Family Geryoniidae Eschscholtz, 1829

Remarks: Following Bentalge *et al.* (2018), the Geryoniidae are here classified as Limnomedusae and not Trachymedusae as done traditionally.

Genus *Geryonia* Péron & Lesueur, 1810

Geryonia Péron & Lesueur, 1810: 329, type species *Geryonia hexaphylla* Péron & Lesueur, 1810.
Carmarina Haeckel, 1864b: 466; type species *Carmarina hastata* Haeckel, 1864 by monotypy.
Geryones Haeckel, 1879: 293; type species *Geryones elephas* Haeckel, 1879 by monotypy.
Carmaris Haeckel, 1879: 296, no type species designated.

Diagnosis: Limnomedusae with gastric peduncle; stomach small, with 6 lips; 6 radial canals, with additional centripetal canals; 6 gonads on radial canals, flattened and leaf-shaped; two kinds of marginal tentacles, solid and hollow; ecto-endodermal statocysts enclosed in mesoglea. No polyp stage, direct developement.

Remarks: *Geryonia hexaphylla* Péron & Lesueur, 1810, a synonym of *Medusa proboscidalis* Forsskål, 1775, was selected by Haeckel (1879) as type of the genus. Mayer (1910: 424) and Kramp (1961) give as type species *Medusa proboscidalis* Forsskål, 1775 for this genus, but this is incorrect as the name was not part of the original nominal species included in *Geryonia* by Péron & Lesueur.

Geryonia proboscidalis (Forsskål, 1775)

Fig. 61A-B

Medusa proboscidalis Forsskål, 1775: 108, pl. 36 fig. 1.
Geryonia hexaphylla Péron & Lesueur, 1810: 329. – Haeckel, 1879: 295, synonym.
Dianaea endrachtensis Quoy & Gaimard, 1824: 566, pl. 84 fig. 2. – Haeckel, 1879: 295, synonym.
Leuckartiara brevicirrata Haeckel, 1864b: 462. – Haeckel, 1879: 295, synonym.
Leuckartiara longicirrata Haeckel, 1864b: 463. – Haeckel, 1879: 295, synonym.
Geryonia umbella Haeckel, 1864b: 464. – Mayer, 1910: 425, synonym.
Geryonia fungiformis Haeckel, 1864b: 465, new name for *Geryonia hexaphylla* Péron & Lesueur, 1810. – Mayer, 1910: 425, synonym.
Geryonia conoides Haeckel, 1864b: 466.
Carmarina hastata Haeckel, 1864b: 467, pl. 11 figs 1-10. – Mayer, 1910: 425, synonym.
Geryones elephas Haeckel, 1879: 294, pl. 18 fig. 7, South Africa.
Geryonia dianaea Haeckel, 1879: 295. – Mayer, 1910: 425, synonym.
Carmaris umbella Haeckel, 1879: 296. – Mayer, 1910: 425, synonym.
Carmaris Giltschii Haeckel, 1879: 296, pl. 18 fig. 8. – Mayer, 1910: 425, synonym.
Geryones mexicana Agassiz & Mayer, 1902: 149, pl. 4 fig. 17. – Mayer, 1910: 425, synonym.
Carmaris rosea Agassiz & Mayer, 1902: 149, pl. 4 fig. 18. – Mayer, 1910: 425, synonym.
Geryonia fungiformis. – Fol, 1873: 471, figs 1-3, pls 24-25, developement.

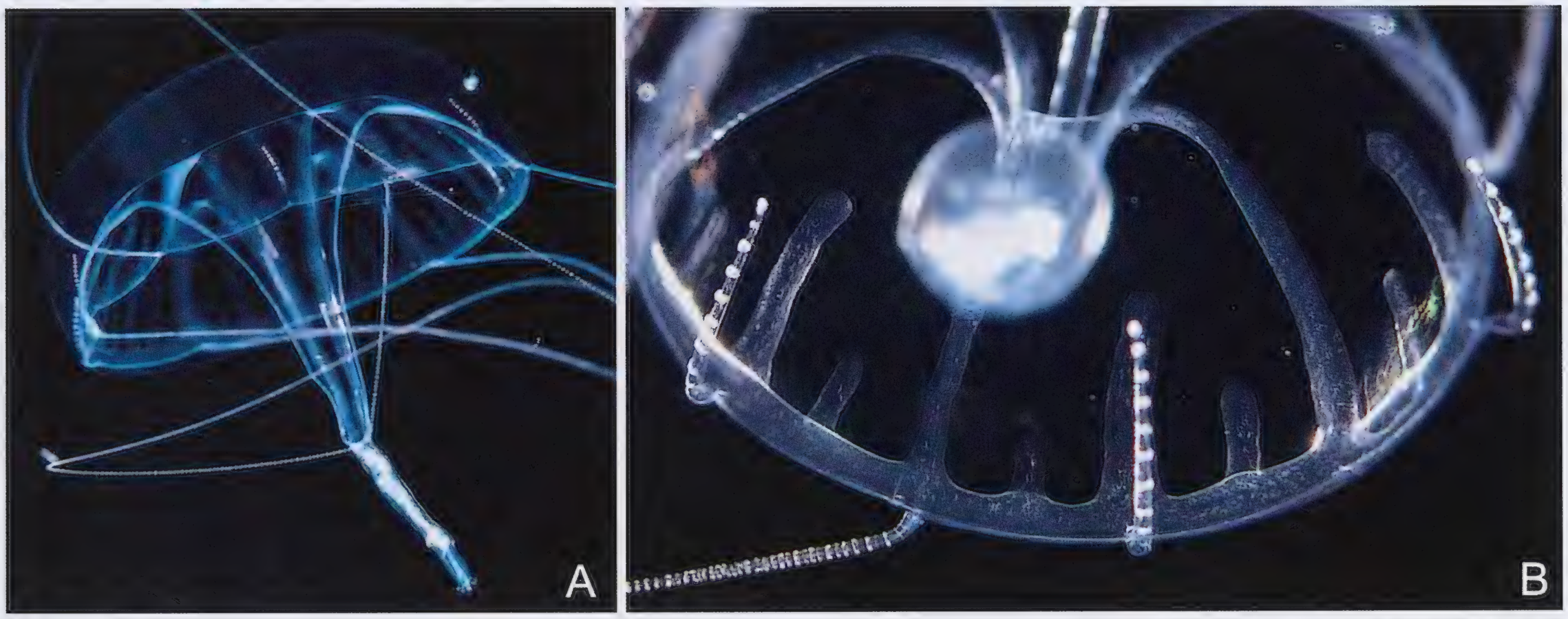


Fig. 61. *Geryonia proboscidalis*. (A) Lateral view of whole, mature animal observed 26-MAR-2019. (B) Bell margin of immature specimen (BFLA4029), bell size approximately 10 mm. Note centripetal canals and the two types of tentacles.

Geryonia proboscidalis. – Haeckel, 1879, 295. – Mayer, 1910: 425, fig. 282, pl. 53 figs 1-3, pl. 43 fig. 10, synonymy. – Berrill, 1950: 296, development. – Kramp, 1959a: 192, fig. 292. – Kramp, 1961: 237. – Kramp, 1968: 122, fig. 332. – Horridge, 1969: 348, figs 5-6, statocysts. – Goy *et al.*, 1991: 119, fig. 47. – Bouillon *et al.*, 2004: 237, fig. 150A-C. – Buecher *et al.*, 2005: 35.

Examined material: BFLA4029; 1 specimen; 04-MAR-2019; diameter 10 mm; part preserved in formalin (UF-013448) and part in alcohol for DNA extraction; 16S sequence MW528644. – 26-MAR-2019; 1 specimen photographed, diameter 20 mm, not collected.
Mediterranean, France, Bay of Villefranche-sur-Mer, 43.6963°N 7.3075°E; 25-APR-2016; diameter 70 mm, photos see DOI: 10.5281/zenodo.53890; whole specimen used for DNA extraction, 16S sequence KX355451.

Description of Florida material: Bell almost hemispherical, 10 to 20 mm wide, jelly thick. Stomach small, on a long conical peduncle, peduncle reaching a length of about twice the bell height (Fig. 61A). Six radial canals, 3-7 centripetal canals betwen pairs of radial canals, ending blindly below apex of subumbrella. Gonads along the six primary radial canals, reaching from circular canal to apex of subumbrella, sheet-like, triangular, pointed end towards circular canal. Two types of tentacles. Six long, perradial tentacles with nematocyst rings, and six short interradial tentacles with adaxial nematocyst clusters, often held upwards adnate to subumbrella (Fig. 61B).

16S Data: The 16S sequence (GMW528644) shows few differences to other published sequences of *G. proboscidalis* (Table 1). The p-distance to the Mediterranean specimen was 0.17%, and 0.33% to the one from Japan. More differences where found with sequence KT809331 (1.2%) originating from the Sea of Cortez (Bastian Bentlage, pers. com.).

Distribution: Occurs in tropical and subtropical parts of all three oceans, including also the Mediterranean, approximately between 35° and 35°S (Kramp, 1957, 1965). Type locality: Mediterranean Sea (Forsskål, 1775).

Remarks: With its six radial canals and the two types of tentacles, *Geryonia proboscidalis* is rather reliably identifiable. It is interesting to note the low 16S sequence divergences observed for the sample from Florida, the Mediterranean, and Japan. *Geryonia proboscidalis* could thus be a good example of a hydromedusan species with a truely circumglobal distribution.

Genus *Liriope* Lesson, 1843

Liriope Lesson, 1843: 331; type species *Liriope cerasiformis* Lesson, 1843 (Haeckel, 1979: 288).
Xanthea Lesson, 1843: 333; type species *Xanthea agaricina* Lesson, 1843 by monotypy.
Leuckartia L. Agassiz, 1862: 364; type species *Leuckartia proboscidalis* L. Agassiz, 1862 by monotypy.
Glossocodon Haeckel, 1864b: 460; type species *Liriope eurybia* Haeckel, 1864 by monotypy.
Glossocodon (*Glossoconus*) Haeckel, 1864b: 461; no type species designated.
Liriantha Haeckel, 1879: 286, no type species designated.
Liriantha (*Lirianthella*) Haeckel, 1879: 286; no type species designated.
Liriantha (*Lirianthissa*) Haeckel, 1879: 287; no type species designated.
Liriope (*Liriopella*) Haeckel, 1879: 289; no type species designated.

Liriope (*Liriopissa*) Haeckel, 1879: 290; no type species designated.
? *Pentaradiata* Zamponi & Gezano, 1989: 34; type species *Pentarradiata estuariensis* Zamponi & Genzano, 1989 by monotypy.
? *Heptarradiata* Zamponi & Gezano, 1989: 35; type species *Heptarradiata rioplatensis* Zamponi & Genzano, 1989 by monotypy.
? *Octorradiata* Zamponi & Gezano, 1989: 36; type species *Octorradiata bonaerensis* Zamponi & Genzano, 1989 by monotypy.

Diagnosis: Limnomedusae with long gastric peduncle; stomach small, with 4 lips; 4 radial canals, with additional centripetal canals; 4 gonads on radial canals, flattened and leaf-shaped; two kinds of marginal tentacles, solid and hollow; ecto-endodermal statocysts enclosed in mesoglea. No polyp stage, direct developement.

Remarks: Rarely, aberrant animals with more than four radial canals and gonads can occur, but the number of oral lips remains rather constantly four (Bouillon *et al.*, 2006).

Liriope tetraphylla (Chamisso & Eysenhardt, 1821)
Fig. 62

Geryonia tetraphylla Chamisso & Eysenhardt, 1821: 357, pl. 27 fig. 2.
Liriope tetraphylla. – Russell, 1953: 419, figs 275-282, pl. 24 fig. 2. – Kramp, 1959a: 193, fig. 293. – Kramp, 1961: 239. – Kramp, 1968: 122, fig. 333. – Pagès *et al.*, 1992: 43, fig. 52. – Nagata *et al.,* 2014: 315, figs 34-35.
For a complete synonymy see Russell (1953).

Examined material: BFLA4026; 1 specimen; 15-FEB-2019; size 20 mm; preserved in alcohol for DNA extraction; 16S sequence MW528649.
MHNG-INVE-0031754; Mediterranean, Bay of Villefranche-sur-Mer; 43.6860°N 7.3170°E; 70 m depth; collection date 11-MAY-2001; >2 specimens; size 3-4 mm; 1 preserved in formalin, others in ethanol for DNA extraction; 16S sequence MW528628.

Observations: Specimen from Florida with nearly hemispherical bell, 20 mm wide, apical jelly thick, with long, thin gastric peduncle, peduncle length more than two times the bell height. Thin nematocysts tracks on exumbrella, four perradial and four interradial, interradial ones reaching only to base of short tentacles, perradial ones longer. Stomach on long gastric peduncle, relatively small, four indistinct perradial lips. Radial canals four, centripetal canals not visible on photos. Gonads very wide, flat, leaf-like, heart-shaped with pointed side pointing toward periphery. Four long perradial tentacles originating at bell margin, with ring-shaped nematocyst clusters. Four short interradial tentacles originating above bell margin on exumbrella, with adaxial nematocyst clusters.

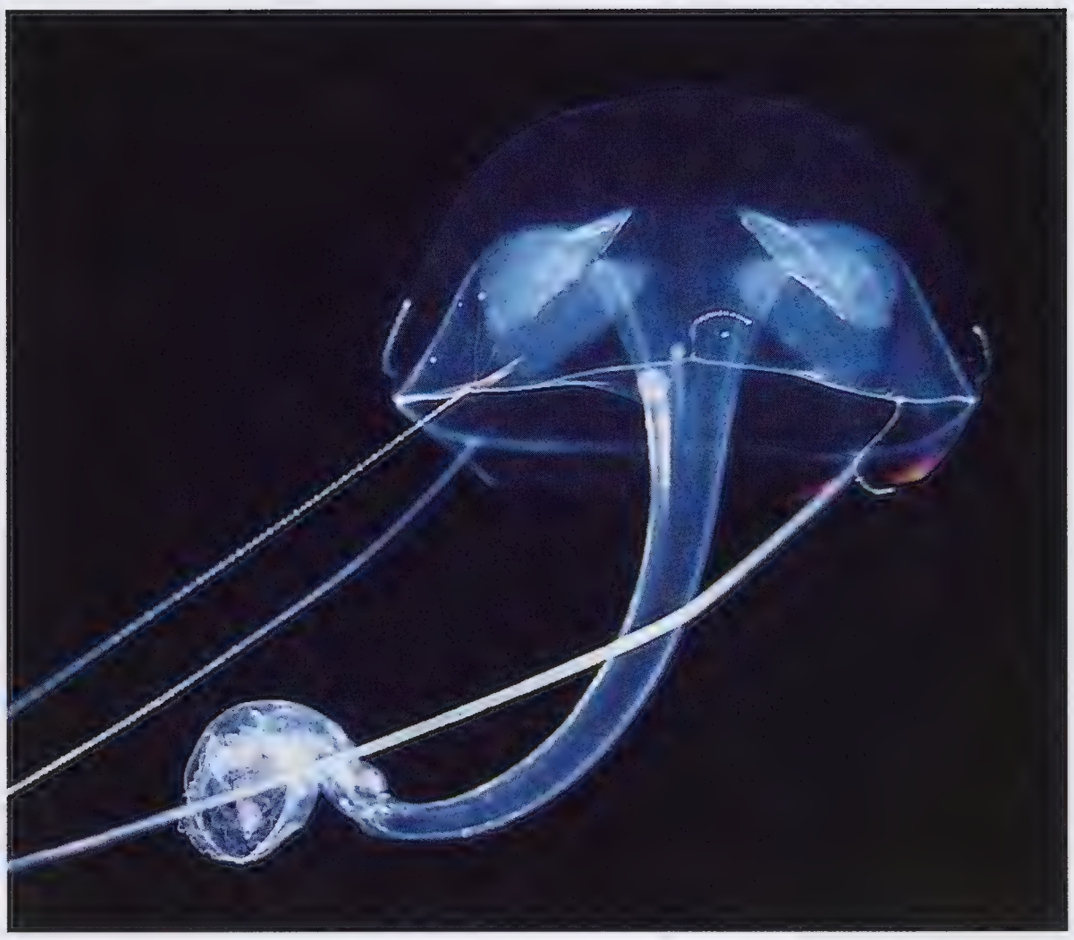


Fig. 62. *Liriope tetraphylla*, BFLA4026, size 20 mm. The stomach is filled with prey items. The larger part of one perradial tentacle is broken off (right).

16S Data: A blastn search in GenBank with the 16S from Florida (MW528649) yielded numerous matches with other *Liriope tetraphylla* samples, but only with identities from 92 to 95.5%. The sequence obtained from the Mediterranean specimen (MW528628) gave identities from 90 to 99 % with other *Liriope tetraphylla* sequences.

Distribution: In Pacific, Indian, and Atlantic ocean, including the Mediterranean, approximately between 40°N and 40°S, in the NE Atlantic reaching to the English Channel (Kramp, 968). Type locality: Indian Ocean (Chamisso & Eysenhardt, 1821).

Remarks: This is a rather unproblematic species, but Collins *et al.* (2008) suggested the existence of cryptic species based on significant divergences in mitochondrial 16S and nuclear sequence data. The high 16S divergences were confirmed in the present study.

Family Olindiidae Haeckel, 1879
Genus *Olindias* Müller, 1861

Olindias Müller, 1861b: 318; type species *Olindias sambaquiensis* Müller, 1861 by monotypy.
Halicalyx Fewkes, 1882a: 277; type species *Halicalyx tenuis* Fewkes, 1882 by monotypy.
Olindioides Goto, 1903: 3, type species *Olindioides formosa* Goto, 1903 by monotypy.

Diagnosis: Olindiidae medusa with 4 radial canals and numerous centripetal canals; numerous tentacles of two kinds: primary ones directed upwards, nematocysts in transverse clasps and often with distal adhesive pads, and secondary ones directed downwards, without adhesive pads, nematocysts in rings. Gonads

on papilliform diverticula of radial canals; numerous marginal bulbs which may transform into tentacles, statocysts usually in pairs at base of primary tentacles. Known hydroid either solitary and lacking tentacles, or forming small stolonal colonies and hydranths with a single filiform tentacle.

Remarks: The grammatical gender of the name is male (Calder, 2010). For descriptions of the hydroid see Weill (1936), Patry *et al.* (2014), and Toshino *et al.* (2019). Toshino *et al.* (2019) provide also a tabular overview on the species of this genus and a phylogenetic tree.

Olindias tenuis (Fewkes, 1882)

Fig. 63A-C

Halicalyx tenuis Fewkes, 1882: 277, pl. 7 fig. 15.
Olindias tenuis. – Bigelow, 1909: 108. – Mayer, 1910: 354, pl. 47 figs 8-10, pl. 48 figs 1-7. – Kramp, 1959a: 173, fig. 244. – Kramp, 1961: 228. – Larson, 1986: 191, fig. 1.
Olindias phosphorica tenuis. – Bigelow, 1938: 113. – Breder, 1956: 13, pls 1-2.
? *Olindias phosphorica.* – Weill, 1936: 1018, fig., hydroid and larva. [not *Olindias phosphorica,* invalid name for *Olindias muelleri* Haeckel, 1879]

Examined material: BFLA4232; 1 specimen, 21-OCT-2019; size 23 mm; part preserved in formalin (UF-013845) and part in alcohol for DNA extraction; 16S sequence MW528688.

Observations: *Olindias* medusa with bell flatter than hemisphere; diameter 23 mm. No exumbrellar pigment bands. Manubrium as long as subumbrellar height, width uniform, cruciform cross-section, mouth with four simple lips. Four radial canals with gonads along distal half to 2/3. Gonads in development with numerous small oogonia, gonads reaching nearly to circular canal, forming numerous diverticula-like outgrowths along entire length of the gonad (Fig. 63A-C), along the windings of the diverticula runs a purple-pinkish stripe (Fig. 63B). 6 to 8 centripetal canals of different lengths per quadrant (Fig. 63A). Tentacles originating from bell margin without distinct bulb formation, two types present (Fig. 63C): about 34 primary tentacles with scattered nematocyst clusters, part of the clusters with characteristic dark pigment; few secondary tentacles with transverse nematocysts rings (some of these tentacles likely broken off), lacking dark pigment, usually pendant. No exumbrellar tentacles. No adhesive pads on tentacles. Bell margin with about 90 bulbs lacking tentacles, with radial band of nematocysts on abaxial side. One to two round statocysts next to primary tentacles (Fig. 63C). Colours: none except for pink stripes on gonad diverticules.

16S Data: A blastn search in GenBank to find matching sequences to the 16S sequence gave a very close match with MG979369, a sequence from a *O. tenuis* originating from the U.S. Virgin Islands (A. G. Collins, pers. comm.). The sequence divergence was only 0.5%.

Distribution: Florida, Bermudas, Bahamas, Puerto Rico (Mayer, 1910; Kramp, 1959a; Larson, 1986). Type locality: USA, Florida, Key West.

Remarks: The present medusa was identified as *O. tenuis* primarily based on it geographic occurrence, but its traits matched the diagnosis of Kramp (1959a) reasonably well [see Table 5 in Toshino *et al.* (2019)]. The species statuses of *O. tenuis* and *O. sambaquinensis* Müller, 1861 have been questioned by e.g. Bigelow (1938) and Kramp (1959a, 1961), considering them either a subspecies or potentially conspecific with *Olindias muelleri* Haeckel, 1879 (using the incorrect name *Olindias phosphorica*, see footnote). The 16S phylogenetic tree presented in Toshino *et al.* (2019) suggests that the three species are distinct.

Although the names *Oceania phosphorica* and its subsequent combination *Olindias phosphorica* have regularly been attributed to Delle Chiaje, Delle Chiaje (1841) credited "Pér" as author of the binomen and he has thus not established a new species. The correct authority of *Oceania phosphorica* is Péron & Lesueur, 1810 (now recognised as a *Clytia* species, *viz.* a synonym of *Clytia hemisphaerica*). Delle Chiaje's (1841) usage of *Oceania phosphorica* is therefore a misapplication and not a valid name for the common Mediterranean *Olindias* species. The species was first correctly named by Haeckel (1879) as *Olindias muelleri*.

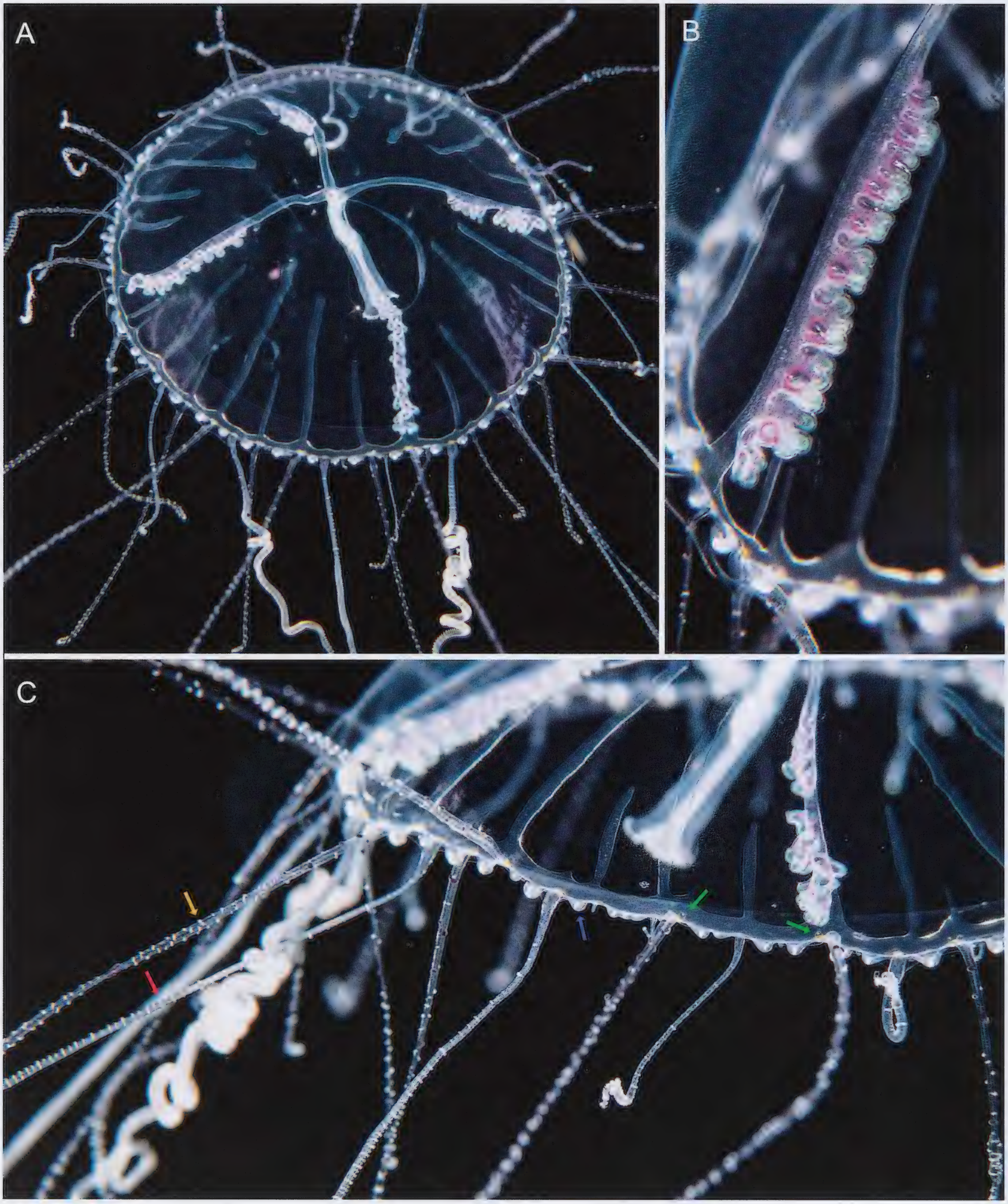


Fig. 63. *Olindias tenuis*, BFLA4232, bell diameter 23 mm. (A) Oblique aboral view of whole animal. (B) Lateral view of radial canal with gonad diverticula. (C) Bell margin with primary tentacles (yellow arrow) and secondary tentacles (red arrow), green arrows point to statocysts. Note the absence of tentacle bulbs, but numerous bulbs without tentacles (blue arrow).

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REFERENCES

Agassiz A. 1862. *In:* Agassiz L. 1862.

Agassiz A. 1865. North American Acalephae. *Illustrated Catalogue of the Museum of Comparative Zoölogy at Harvard College* 2: 1-234.

Agassiz A., Mayer A.G. 1899. Acalephs from the Fiji Islands. *Bulletin of the Museum of comparative Zoölogy of Harvard* College 32(9): 157-189, pls 1-17.

Agassiz A., Mayer A. G. 1902. Medusae. Report of the scientific research expedition to the tropical Pacific. U.S. Fish Comm. St. Albatross, 1899-1900. III. *Memoirs of the Museum of Comparative Zoology at Harvard College* 26: 136-176, pls 1-14.

Agassiz L. 1862. *Contributions to the natural history of the United States of America. Vol. IV*. Little Brown, Boston, pp. 1-380, pls 1-19.

Akiyama H., Yamazaki Y., Kubota S. 2013. Second record of *Thecocodium quadratum* (Hydrozoa, Anthomedusae, Ptilocodiidae) in Japan. *Bulletin of the Biogeographical Society of Japan* 68: 113-115.

Allman G.J. 1863. Notes on the Hydroida. I. On the structure of *Corymorpha nutans*. II. Diagnoses of new species of Tubularidae obtained, during the autumn of 1862, on the coasts of Shetland and Devonshire. *Annals and Magazine of Natural History* (3)11(61): 1-12.

Allman G.J. 1872. A monograph of the gymnoblastic or tubularian hydroids. Conclusion of Part I, and Part II, containing descriptions of the genera and species of Gymnoblastea. *Ray Society, London*, pp. 155-450, pls 1-23.

Allman G.J. 1877. Report on the Hydroida collected during the Exploration of the Gulf Stream by L. F. de Pourtalès, Assistant United States Coast Survey. *Memoirs of the Museum of Comparative Zoology* 5(2): 1-66, pls 1-34.

Allwein J. 1967. North American hydromedusae from Beaufort, North Carolina. *Videnskabelige meddelelser fra Dansk naturhistorik Forening* 130: 117-136.

Altuna Ã. 2016. The life cycle of symbiotic *Zanclea sessilis* (Hydrozoa: Zancleidae) colonies with polymorphic hydranths from the Bay of Biscay. *Marine Biodiversity* 46(4): 901-910.

Ames C.L., Ohdera A.H., Colston S.M., Collins A.G., Fitt W.K., Morandini A., Erickson J.S., Vora G.J. 2021. Fieldable Environmental DNA Sequencing to Assess Jellyfish Biodiversity in Nearshore Waters of the Florida Keys, United States. *Frontiers in Marine Science* 8(369): 1-17.

Andrade L., Migotto A. 1997. Is there a link between *Hebella* Hydroids (Hydrozoa, Lafoeidae) and *Staurodiscus* medusae (Hydrozoa, Laodiceidae)? *Resumos expandidos do VII COLACMAR Congresso Latino-Americano sobre Ciências do Mar*, I: 35-36.

AntWeb 2021. Available from http://www.antweb.org. Accessed 24 April 2021.

Arai M.N., Brinckmann-Voss A. 1980. Hydromedusae of British Columbia and Puget Sound. *Canadian Bulletin of Fisheries and Aquatic Sciences* 204: 1-192.

Bale W. M. 1888. On some new and rare Hydroida in the Australian Museum collections. *Proceedings of the Linnean Society of New South Wales* ser. 2 volume 3: 745-799, pls 12-21.

Benovic A., Lucic D., Onofri V., Batistic M., Njire J. 2005. Bathymetric distribution of medusae in the open waters of the middle and south Adriatic Sea during spring 2002. *Journal of Plankton Research* 27(1): 79-89.

Bentlage B., Osborn K.J., Lindsay D.J., Hopcroft R.R., Raskoff K.A., Collins A.G. 2018. Loss of metagenesis and evolution of a parasitic life style in a group of open-ocean jellyfish. *Molecular Phylogenetics and Evolution* 124: 50-59.

Berrill N.J. 1950. Development and medusa-bud formation in the hydromedusae. *Quarterly Review of Biology* 25(3): 292-316.

Bigelow H.B. 1904. Medusae from the Maldive Islands. *Bulletin of the Museum of Comparative Zoology at Harvard College* 39(9): 245-269, pls 1-17.

Bigelow H.B. 1909. The Medusae. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer "Albatross" from October, 1904, to March, 1905. XVI. *Memoirs of the Museum of comparative Zoology at Harvard College* 37: 1-243, pls 1-48.

Bigelow H.B. 1913. Medusae and Siphonophora collected by the U.S. steamer "Albatross" in the Northwestern Pacific. *Proceedings of the United States National Museum* 44: 1-119, pls 1-6.

Bigelow H.B. 1917. Exploration of the coast water between Cape Cod and Halifax in 1914 and 1915, by the U.S. Fisheries schooner Grampus. Oceanography and plankton. *Bulletin of the Museum of Comparative Zoology at Harvard College* 61(8): 161-357.

Bigelow H.B. 1918. Some Medusae and Siphonophora from the western Atlantic. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 62: 363-442, pls 1-8.

Bigelow H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bulletin of the Bureau of Fisheries* 40(2): 1-509.

Bigelow H.B. 1928. Hydromedusae, siphonophores and ctenophores of the "Albatross" Philippine Expedition. *In:* Contributions to the biology of the Philippine Archipelago and adjacent region. *Bulletin United States National Museum* 100(1): 279-362, pls 39-43.

Bigelow H. B. 1938. Medusae taken during the years 1929 and 1930. Plankton of the Bermuda Oceanographic Expeditions. VIII. *Zoologica*, N.Y. 23: 99-189.

Blackburn M. 1938. Hydrozoa. *In:* The Sir Joseph Banks Islands. Reports of the expedition of the McCoy Society for Field Investigation and Research, 3. *Proceedings of the Royal Society of Victoria, new series* 50: 312-328.

Bleeker J., Van Der Spoel S. 1988. Medusae of the Amsterdam Mid North Atlantic Plankton Expeditions (1980-1983) with description of two new species. *Bijdragen tot de Dierkunde* 58(2): 227-258.

Boero F., Bouillon J. 1989. The life cycles of *Octotiara russelli*

and *Stomotoca atra* (Cnidaria, Anthomedusae, Pandeidae). *Zoologica Scripta* 18(1): 1-7.

Boero F., Bouillon J., Gravili C. 1991. The life cycle of *Hydrichthys mirus* (Cnidaria: Hydrozoa: Anthomedusae: Pandeidae). *Zoological Journal of the Linnean Society* 101(2): 189-199.

Boero F., Bouillon J., Kubota S. 1997. The medusae of some species of *Hebella* Allman, 1888 and *Anthohebella* gen. nov. (Cnidaria, Hydrozoa, Lafoeidae), with a world synopsis of species. *Zoologische Verhandelingen, Leiden* 310: 1-53.

Boero F., Bouillon J., Gravili, C. 2000. A survey of *Zanclea*, *Halocoryne* and *Zanclella* (Cnidaria, Hydrozoa, Anthomedusae, Zancleidae) with description of new species. *Italian Journal of Zoology* 67: 93-124.

Boissin E., Hoareau T.B., Postaire B., Gravier-Bonnet N., Bourmaud C.A.F. 2018. Cryptic diversity, low connectivity and suspected human-mediated dispersal among 17 widespread Indo-Pacific hydroid species of the south-western Indian Ocean. *Journal of Biogeography* 45(9): 2104-2117.

Bolton B. 2021. An online catalog of the ants of the world. Available from http://antcat.org (accessed 24 April 2021)

Bouillon J. 1967. Révision de la famille des Ptilocodiidae avec la description d'un nouveau genre et d'une nouvelle espèce. *Bulletin de la classe des sciences de l'Académie royale de Belgique* 53(9): 1106-1131.

Bouillon J. 1978a. Hydroméduses de l'Archipel des Séchelles et du Mozambique. *Revue de Zoologie Africaine* 92(1): 117-172.

Bouillon J.1978b. Hydroméduses de la mer de Bismarck (Papouasie, Nouvelle-Guinée). Partie 1: Anthomedusae Capitata (Hydrozoa - Cnidaria). *Cahiers de Biologie Marine* 19(3): 249-297.

Bouillon J. 1978c. Hydroméduses de la mer de Bismarck (Papouasie, Nouvelle-Guinée). II. Limnomedusa, Narcomedusa, Trachymedusa et Laingiomedusa (sous classe nouv.). *Cahiers de Biologie Marine* 19: 473-483.

Bouillon J. 1980. Hydroméduses de la Mer de Bismarck. (Papouasie Nouvelle-Guinée). Partie 3: Anthomedusae - Filifera (Hydrozoa - Cnidaria). *Cahiers de Biologie Marine* 21(3): 307-344.

Bouillon J. 1984a. Revision de la famille des Phialuciidae (Kramp, 1955) (Leptomedusae, Hydrozoa, Cnidaria), avec un essai de classification des Thecatae-Leptomedusae. *Indo-Malayan Zoology* 1(1): 1-24.

Bouillon J. 1984b. Hydroméduses de la Mer de Bismarck (Papouasie Nouvelle-Guinée). Partie IV: Leptomedusae (Hydrozoa - Cnidaria). *Indo-Malayan Zoology* 1(1): 25-112.

Bouillon J. 1985. Notes additionelles sur les hydroméduses de la mer de Bismarck (Hydrozoa-Cnidaria). *Indo-Malayan Zoology* 2(2): 245-266.

Bouillon J. 1987. Considérations sur le développement des Narcoméduses et sur leur position phylogénétique. *Indo-Malayan Zoology* 4: 189-278.

Bouillon J. 1999. Hydromedusae (pp. 385-465). *In:* Boltovskoy D. (Ed.), South Atlantic zooplankton, vol. 1,. *Backhuys, Leiden.*

Bouillon J., Barnett T.J. 1999. The marine fauna of New Zealand: Hydromedusae (Cnidaria: Hydrozoa). *Niwa Biodiversity Memoir* 113: 1-136.

Bouillon J., Seghers G., Boero F. 1988a. Note sur les cnidocystes des hydroméduses de la mer de Bismarck (Papouasie-Nouvelle Guinée). *Indo-Malayan Zoology* 5(2): 203-224.

Bouillon J., Seghers G., Boero F. 1988b. Notes additionnelles sur les méduses de Papouasie Nouvelle-Guinée (Hydrozoa, Cnidaria). 3. *Indo-Malayan Zoology* 5(2): 225-253.

Bouillon J., Boero F., Seghers G. 1991. Notes additionnelles sur les méduses de Papouasie Nouvelle-Guinée (Hydrozoa, Cnidaria) 4. *Cahiers de Biologie Marine* 32: 387-411.

Bouillon J., Medel M.D., Pagès F., Gili J.M., Boero B., Gravili C. 2004. Fauna of the Mediterranean Hydrozoa. *Scientia Marina* 68 (Suppl. 2): 1-448.

Bouillon J., Gravili C., Pages F., Gili J.M., Boero F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle* 194: 1-591.

Brandt J.F. 1834-1835. Prodromus descriptionis animalium ab H. Mertensio in orbis terrarum circumnavigatione observatorum. Fascic. I., Polypos, Acalephas Discophoras et Siphonophoras, nec non Echinodermata continens / auctore, Johanne Friderico Brandt. *Recueil des Actes des séances publiques de l'Académie impériale des Sciences de St. Pétersbourg* 1834: 201-275.

Brandt J.F. 1837. Remarques sur quelques modifications dans l'arrangement de l'ordre des Acalèphes discophores ou Ombellifères. *Bulletin scientifique publié par l'Académie impériale des sciences de St. Pétersbourg* 1(24): 185-191.

Brandt J.F. 1838. Ausführliche Beschreibung der von C. H. Mertens auf seiner Weltumsegelung beobachteten Schwimmquallen. *Mémoires de l'Académie impériale des sciences de St.-Pétersbourg* (6)2: 237-412.

Breder C.M. Jr. 1956. Notes on the behavior and habits of the medusa, *Olindias phosphorica tenuis* Fewkes. *Zoologica, N.Y.* 41(1): 13-15.

Brinckmann-Voss A. 1967. The hydroid of *Vannuccia forbesii* (Anthomedusae, Tubulariidae). *Breviora* 263: 1-10.

Brinckmann-Voss A. 1970. Anthomedusae/Athecata (Hydrozoa, Cnidaria) of the Mediterranean. Part I. Capitata. *Fauna e Flora Golfo di Napoli* 39: 1-96, pls 1-11.

Brinckmann-Voss A., Arai M.N. 1998. Further notes on Leptolida (Hydrozoa: Cnidaria) from Canadian Pacific waters. *Zoologische Verhandelingen* 323: 37-68.

Brooks W.K. 1880. Budding in free Medusae. *American Naturalist* 14: 670-671.

Brooks W.K. 1883. List of medusae found at Beaufort, N.C., during the summers of 1880 and 1881. *Studies from the Biological Laboratory, Johns Hopkins University* 2(2): 135-146.

Brooks W.K. 1886. The life history of the Hydromedusae. A discussion of the origin of the medusae and the significance of metagenesis. *Memoirs of the Boston Society of Natural History* 111: 359-430, pls 27-44.

Brooks W.K., Rittenhouse S. 1907. On *Turritopsis nutricula* (McCrady). *Proceedings of the Boston Society of Natural History* 33: 429-460, pls 30-35.

Browne E.T. 1905. Hydromedusae with a revision of the Williadae and Petasidae. *Fauna and geography Maldives and Laccadives Archipelagoes* 2(3): 722-749, pls 54-57.

Browne E.T. 1907. The Hydroida collected by the Huxley from northside of the Bay of Biscay in August, 1906. *Journal of the Marine Biological Association of the U. K.* 8: 15-37, pls 1-2.

Browne E.T. 1916. Medusae from the Indian Ocean (collected by Prof. Stanley Gardiner in H.M.S. Sealark in 1905). *In:* The Percy Sladen Trust Expedition to the Indian Ocean in 1905). *Transactions of the Linnean Society of London, Zoology* 17: 169-209.

Buecher E., Gibbons M.J. 2003. Observations on the diel

vertical distribution of Hydromedusae in the southern Benguela. *African Journal of Marine Science* 25: 231-238.

Buecher E., Goy J., Gibbons M.J. 2005. Hydromedusae of the Agulhas Current. *African Invertebrates* 46: 27-69.

Calder D.R. 1970. North American record of the hydroid *Proboscidactyla ornata* (Hydrozoa, Proboscidactylidae). *Chesapeake Science* 11(2): 130-132.

Calder D.R. 1971. Hydroids and hydromedusae of southern Chesapeake Bay. *Virginia Institute of Marine Science, Special Papers in Marine Science* 1: 1-125.

Calder D.R. 1988. Shallow-water hydroids of Bermuda. The Athecatae. *Royal Ontario Museum Life Sciences Contributions* 148: 1-107.

Calder D.R. 1991. Shallow-water hydroids of Bermuda: the Thecatae, exclusive of Plumularioidea. *Royal Ontario Museum Life Sciences Contributions* 154: 1-140.

Calder D.R. 2010. Some anthoathecate hydroids and limnopolyps (Cnidaria, Hydrozoa) from the Hawaiian archipelago. *Zootaxa* 2590: 1-91. DOI: 10.11646/zootaxa.2590.1.1

Calder D.R. 2013. Some shallow-water hydroids (Cnidaria: Hydrozoa) from the central east coast of Florida, USA. *Zootaxa* 3648: 1-72. DOI: 10.11646/zootaxa.3648.1

Calder D.R. 2019. On a collection of hydroids (Cnidaria, Hydrozoa) from the southwest coast of Florida, USA. *Zootaxa* 4689(1): 1-141. DOI: 10.11646/zootaxa.4689.1.1

Canudas Gonzàlez A. 1979. Contribución al conocimiento de las medusas (Coelenterata) de la Laguna de Términos, Campeche, México. *Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México* 6(1): 83-188.

Cerrano C., Amoretti D., Bavestrello G. 1997. The polyp and the medusa of *Zanclea costata* Gegenbaur (Cnidaria, Hydrozoa). *Italian Journal of Zoology* 64: 177-180.

Chamisso A.V., Eysenhardt C.G. 1821. De animalibus quibusdam e classe vermium Linneana... *Nova Acta physico-medica Academiae Cesareae Leopoldino-Carolinae* 10(2): 345-374, pls 24-33.

Clarke S.F. 1882. New and interesting hydroids from Chesapeake Bay. *Memoirs read before the Boston Society of Natural History* 3(4): 135-142, pls 7-9.

Collins A.G., Bentlage B., Lindner A., Lindsay D., Haddock S.H.D., Jarms G., Norenburg J.L., Jankowski T., Cartwright P. 2008. Phylogenetics of Trachylina (Cnidaria: Hydrozoa) with new insights on the evolution of some problematical taxa. *Journal of the Marine Biological Association of the U. K.* 88(8): 1673-1685.

Cornelius P.F.S. 1982. Hydroids and medusae of the family Campanulariidae recorded from the eastern north Atlantic, with a world synopsis of genera. *Bulletin of the British Museum, Zoology* 42(2): 37-148.

Cornelius P.F.S. 1995. North-west European thecate hydroids and their medusae. Part 1. Introduction, Laodiceidae to Haleciidae. *Synopses of the British Fauna New Series* 50(1): 1-347.

Coward W.E. 1909. On *Ptilocodium repens*, a new gymnoblastic hydroid epizoic on a pennatulid. *Proceedings Koninklijke Nederlandsche Akademie van Wetenschappen Amsterdam, Sect. Sci.* 17(2): 635-641, pl. 1.

Cunha A.F., Collins A.G., Marques A.C. 2017. Phylogenetic relationships of Proboscoida Broch, 1910 (Cnidaria, Hydrozoa): Are traditional morphological diagnostic characters relevant for the delimitation of lineages at the species, genus, and family levels? *Molecular Phylogenetics and Evolution* 106: 118-135.

Dawson M. N. 2004. Some implications of molecular phylogenetics for understanding biodiversity in jellyfishes, with emphasis on Scyphozoa. *Hydrobiologia* 531: 249-260.

De Blainville H.M.D. 1834. Manuel d'actinologie ou de zoophytologie, 2 vols. *F. G. Levrault, Paris*, 695 pp., pls 1-99.

Du F., Xu Z., Huang J., Guo D. 2010. New records of medusae (Cnidaria) from Daya Bay, northern South China Sea, with descriptions of four new species. *Proceedings of the Biological Society of Washington* 123(1): 72-86.

Eschscholtz F. 1829. System der Acalephen. Eine ausführliche Beschreibung aller medusenartigen Strahltiere. *Ferdinand Dümmler, Berlin*, 190 pp., 16 pls.

Eydoux F., Soulyet L.F.A. 1841-1852. Voyage autour du monde, exécuté pendant les années 1836 et 1837 sur la corvette La Bonite, commandée par M. Vaillant. Zoologie. *Arthus Bertrand, Paris*, Vol. 2. DOI: 10.5962/bhl.title.10814

Fagetti G.E. 1973. Medusas de aguas chilenas. *Revista de Biología Marina.* 15(1): 31-75.

Fewkes J.W. 1881. Studies of the Jelly-fishes of Narragansett Bay. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 8: 141-182, pls 1-10.

Fewkes J.W. 1882a. Notes on acalephs from the Tortugas, with a description of new genera and species. *In:* Explorations of the surface fauna of the Gulf Stream, under the auspices of the U.S. Coast Survey, by Alexander Agassiz. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 9(7): 251-289, pls 1-7.

Fewkes J.W. 1882b. On the Acalephae of the East coast of New-England. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 9(8): 291-310, pl. 1.

Fewkes J.W. 1887. A hydroid parasitic on a fish. *Nature, London* 36: 604-605.

Fol H. 1873. Die erste Entwickelung des Geryonideneies. *Jenaer Zeitschrift für Naturwissenschaften* 7: 471-492, pls 24-25.

Forbes E. 1848. A monograph of the British naked-eyed medusae: with figures of all the species. *Ray Society, London.* pp. 104, 13 plates.

Forbes E., Goodsir J. 1853. On some remarkable marine Invertebrata new to the British Seas. *Transactions of the Royal Society of Edinburgh* 20: 307-315.

Forsskål P. in: Niebuhr C.E. 1775. Descriptiones animalium avium, amphibiorium, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr. *Mölleri, København*, 164 pp. DOI: 10.5962/bhl.title.2154

Fraser C.M. 1912. Some hydroids of Beaufort, North Carolina. *Bulletin of the Unites States Bureau of Fisheries* 30: 337-387.

Galea H.R. 2007. Hydroids and hydromedusae (Cnidaria: Hydrozoa) from the fjords region of southern Chile. *Zootaxa* 1597: 1-116.

Galea H.R. 2008. On a collection of shallow-water hydroids (Cnidaria: Hydrozoa) from Guadeloupe and Les Saintes, French Lesser Antilles. *Zootaxa* 17: 1-54.

Galea H.R. 2010. Additional shallow-water thecate hydroids (Cnidaria: Hydrozoa) from Guadeloupe and Les Saintes, French Lesser Antilles. *Zootaxa* 2570: 1-40.

Gegenbaur C. 1854. Zur Lehre vom Generationswechsel und der Fortpflanzung bei Medusen und Polypen. *Verhandlun-*

gen der Physikalisch-Medizinischen Gesellschaft zu Würzburg 4: 154-221, pls 1-2. [page numbering in reprint differs]

Gegenbaur C. 1857. Versuch eines Systems der Medusen, mit Beschreibung neuer oder wenig gekannter Formen; zugleich ein Beitrag zur Kenntnis der Fauna des Mittelmeeres. *Zeitschrift für wissenschaftliche Zoologie* 8: 202-273, pls 7-9.

Gershwin L.A., Zeidler W. 2003. Encounter 2002 expedition to the Isles of St Francis, South Australia: Medusae, siphonophores and ctenophores. *Transactions of the Royal Society of South Australia* 127: 205-241.

Gershwin L.-A., Zeidler W., Davie P.J.F. 2010. Medusae (Cnidaria) of Moreton Bay, Queensland, Australia. *Memoirs of the Queensland Museum* 54(3): 47-108.

Gmelin J. F. 1788. Caroli a Linné ... Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis / cura Jo. Frid. Gmelin. Tom. 1, Pars. 6. *Impensis Georg. Emanuel. Beer, Lipsiae,* pp. 3021-3909.

Gosse P.H. 1853. A naturalist's rambles on the Devonshire coast. *John van Voorst, London*, i-xvi, 1-451, pls 1-28.

Goto S. 1903. The Craspedote medusa *Olindias* and some of its natural allies. *Mark Anniversary Volume* art. 1: 1-22, pls 1-3. DOI: 10.5962/bhl.title.1719

Govindarajan A.F., Boero F., Halanych K.M. 2006. Phylogenetic analysis with multiple markers indicates repeated loss of the adult medusa stage in Campanulariidae (Hydrozoa, Cnidaria). *Molecular Phylogenetics and Evolution* 38: 820-834.

Goy J. 1979. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961-1962). 35. Méduses. *Annales de l'Institut Océanographique* 55 (Suppl.): 263-296.

Goy J., Lakkis S., Zeidane R. 1991. Les méduses (Cnidaria) des eaux Libanaises. *Annales de l'Institut Océanographique de Paris* 67: 99-128.

Gravili C., Bouillon J., D'elia A., Boero F. 2007. The life cycle of *Gastroblasta raffaelei* (Cnidaria, Hydrozoa, Leptomedusae, Campanulariidae) and a review of the genus *Gastroblasta*. *Italian Journal of Zoology* 74(4): 395-403.

Haeckel E. 1864a. Beschreibung neuer Craspedoter Medusen aus dem Golfe von Nizza. *Jenaische Zeitschrift für Medizin und Naturwissenschaft* 1: 326-342. https://www.biodiversitylibrary.org/page/8620986

Haeckel E. 1864b. Die Famile der Rüsselquallen (Medusae, Geryonidae). *Jenaische Zeitschrift für Medizin und Naturwissenschaften* 1: 435-461, pls 11-12.

Haeckel E. 1879. Das System der Medusen. Erster Teil einer Monographie der Medusen. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 1: I-XX, 1-360, 20 pls.

Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.

Hammer W.M. 1975. Underwater observations of blue-water plankton: Logistics, techniques, and safety procedures for divers at sea. *Limnology and Oceanography* 20(6): 1045-1051.

Hamond R. 1974. Some medusae and other Hydrozoa from the Indian Ocean and the Bass Strait. *Journal of natural History* 8(5): 549-561.

Hand C. 1954. Three Pacific species of "*Lar*" (including a new species). Their hosts, medusae, and relationships (Coelenterata, Hydrozoa). *Pacific Science* 8(1): 51-67.

Hand C., Hendrickson J.R. 1950. A two-tentacled, commensal hydroid from California (Limnomedusae, Proboscidactyla). *Biological bulletin of the Marine Biological Laboratory / Woods Hole* 99(1): 74-87.

Hartlaub C. 1907. XII Craspedote Medusen. Teil 1, Lieferung 1. Codoniden und Cladonemiden. *Nordisches Plankton* 6: 1-135.

Hartlaub C. 1914. Craspedote Medusen. Teil 1, Lieferung 3, Tiaridae. *Nordisches Plankton* 6: 237-363.

Hirose M., Hirose E. 2012. A new species of *Zanclea* (Cnidaria: Hydrozoa) associated with scleractinian corals from Okinawa, Japan. *Journal of the Marine Biological Association of the U. K.* 92: 877-884.

Horridge G.A. 1969. Statocysts of medusae and evolution of stereocilia. *Tissue & Cell* 1: 341-353.

Huang J.Q., Xu Z.Z., Lin J.Z., Qiu M.F. 2008. Three new species of Anthomedusae (Hydrozoa, Hydroidomedusae) from the Fujian sea water. *Journal of Xiamen University Natural Science* 47(3): 408-412.

Huang J.-Q, Xu Z.-Z. & Lin M. 2015. *In:* Huang J.-Q., Xu Z.-Z., Lin M., Gua D.-H. 2015. Two New Species of Suborder Tubulariida from the South China Sea (Anthomedusae, Capitata). *Journal of Xiamen University (Natural Science)* 54(6): 824-828.

ICZN. The International Code of Zoological Nomenclature. Available at https://www.iczn.org qdd3ww3e accessed May April 2021

Jarms G. 1987. *Thecocodium quadratum* (Werner 1965) redescribed, *T. penicillatum* sp. nov., and a method for rearing hydrozoans (pp. 57-66). *In:* Bouillon J., Boero F., Cicogna F., Cornelius P.F.S. (eds), Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae. *Clarendon Press, Oxford.*

Johnson M., Zaretskaya I., Raytselis Y., Merezhuk Y., Mcginnis S., Madden T.L. 2008. NCBI BLAST: a better web interface. *Nucleic Acids Research* 36(suppl. 2): W5-W9. DOI: 10.1093/nar/gkn201

Johnston G. 1836. A catalogue of the zoophytes of Berwickshire. *History of the Berwickshire Naturalists' Club* 1: 107-108.

Keferstein W., Ehlers E. 1861. Zoologische Beiträge gesammelt in Winter 1859-1860 in Neapel und Messina, *Leipzig*, viii + 112 pp., 15 pls. DOI: 10.5962/bhl.title.4760

Keller C. 1883. Untersuchungen über neue Medusen aus dem Rothen Meere. *Zeitschrift für wissenschaftliche Zoologie* 38: 621-670.

Keller C. 1884. Mittheilungen über Medusen. *Recueil zoologique Suisse* 1: 403-422, pl. 21.

Kölliker A. 1853. *In:* Gegenbaur C., Kölliker A. Müller H. 1853. Bericht über einige im Herbste 1852 angestellte vergleichend-anatomische Untersuchungen. *Zeitschrift für wissenschaftliche Zoologie* 4: 299-370.

Kramp P.L. 1928. Hydromedusae 1. Anthomedusae. *In:* Papers from Dr. Mortensen's Pacific Expeditions 1914-1916, XLIII. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 85: 27-64.

Kramp P.L. 1947. Medusae. Part III. Trachylina and Scyphozoa, with zoogeographical remarks on all the medusae of the northern Atlantic. *Danish Ingolf Expedition* 5(14): 1-66.

Kramp P.L. 1948. Trachymedusae and Narcomedusae from the "Michael Sars" North Atlantic deep-sea Expedition 1910, with additions on Anthomedusae, Leptomedusae, and

Scyphomedusae. *Report on the scientific results of the "Michael Sars" north Atlantic deep-sea expedition 1910...* 5(9): 1-23, pl. 1.

Kramp P.L. 1953. Hydromedusae. *Scientific Report of the Great Barrier Reef Expedition* 6(4): 259-322.

Kramp P.L. 1955a. A revision of Ernst Haeckel's determinations of a collection of Medusae belonging to the Zoological Museum of Copenhagen. *Deep Sea Research* 3: 149-168.

Kramp P.L. 1955b. The medusae of the tropical west coast of Africa. *Atlantide Report* 3: 239-324, pls 1-3.

Kramp P.L. 1957. Hydromedusae from the Discovery collections. *Discovery Reports* 29: 1-128.

Kramp P.L. 1959a. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report* 46: 1-283.

Kramp P.L. 1959b. Some new and little known Indo-Pacific medusae. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 121: 223-259.

Kramp P.L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the U. K.* 40: 1-469.

Kramp P.L. 1962. Medusae of Vietnam. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 124: 305-366.

Kramp P.L. 1965. The hydromedusae of the Pacific and Indian oceans. Dana Report 63: 1-162.

Kramp P.L. 1968. The hydromedusae of the Pacific and Indian oceans. Sections II and III. *Dana Report* 72: 1-200.

Kramp P. L., Damas D. 1925. Les méduses de la Norvège. Introduction et partie spéciale. *Videnskabelige meddelelser fra Dansk naturhistorik Forening* 80: 217-323.

Kubota S. 1993. The medusa of *Thecocodium quadratum* (Werner) (Anthomedusae, Ptilocodiidae) from southern Japan. *Publications of Seto Marine Biological Laboratory* 36(1-2): 89-92.

Kubota S., Kitada H., Yamada T., Okuizumi K. 2011. Rediscovery of *Pandeopsis ikarii* (Cnidaria, Hydrozoa) from the type locality after 83 years and a new locality record from northern Japan, with reference to a new GFP distribution pattern. *Bulletin of the Biogeographical Society of Japan* 20: 57-60.

Kubota S., Hui-Tai L.T., Tan W. 2018. Occurrence of a rare *Thecocodium* Medusa (Anthomedusae, Ptilocodiidae) From Taiwan. *Kuroshio Biosphere* 14: 7-9.

Kubota S., Meldonian S. 2016. First Occurrence of a Rare *Thecocodium* Medusa (Anthomedusae, Ptilocodiidae) from Riviera Beach, Florida, USA. *Biogeography* 18: 77-78.

Lamouroux J.V.F. 1812. Extrait d'un mémoire sur la classification des polypes coralligènes non entièrement pierreux. *Nouveau Bulletin des Sciences par la Société Philomatique de Paris* 3(63): 181-188.

Lang A. 1886. *Gastroblasta Raffaelei.* Eine durch eine Art unvollständiger Theilung entstehende Medusen-Kolonie. *Jenaische Zeitschrift für Naturwissenschaft* 19: 735-763, pls 20-21.

Larkin M.A., Blackshields G., Brown N.P., Chenna R., Mcgettigan P.A., Mcwilliam H., Valentin F., Wallace I.M., Wilm A., Lopez R., Thompson J.D., Gibson T.J., Higgins D.G. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23(21): 2947-2948.

Larson R.J. 1982. Life history of the hydromedusa *Stomotoca pterophylla* Haeckel and its ichtyoparasitic hydroid. *Smithsonian contributions to the marine sciences* 12: 433-439.

Larson R.J. 1986. Observations on the light-inhibited activity cycle and feeding behaviour of the hydromedusa *Olindias tenuis*. *Uitgaven Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen* 118: 191-199.

Larson R.J., Harbison G.R. 1990. Medusae from McMurdo Sound, Ross Sea, including the descriptions of two new species, *Leuckartiara brownei* and *Benthocodon hyalinus*. *Polar Biology* 11: 19-25.

Larson R.J., Mills C.E., Harbison G. R. 1989. In situ foraging and feeding behaviour of Narcomedusae (Cnidaria: Hydrozoa). *Journal of the Marine Biological Association of the U. K.* 69: 785-794.

Larson R.J., Mills C.E., Harbison G.R. 1991. Western Atlantic midwater hydrozoan and scyphozoan medusae: in situ studies using manned submersibles. *Hydrobiologia* 216-217: 311-317.

Lesson R.-P. 1830. Zoologie. *In:* Duperrey L.-I., Zoologie by P. R. Lesson and P. Garnot, (eds), Voyage autour du monde, exécuté par ordre du roi, sur la corvette de Sa Majesté, la Coquille, pendant les années 1822, 1823, 1824 et 1825, 2 volumes and atlas. *Paris*. DOI: 10.5962/bhl.title.57936

Lesson R.P. 1843. Histoire naturelle des zoophytes. Acalèphes. *Librairie Encyclopédique de Roret*, *Paris*, 596 pp. DOI: 10.5962/bhl.title.4799

Leuckart R. 1856. Beiträge zur Kenntniss der Medusenfauna von Nizza. *Archiv für Naturgeschichte* 22(1): 1-40, pls 1-2.

Lindner A., Migotto A.E. 2002. The life cycle of *Clytia linearis* and *Clytia noliformis*: metagenic campanulariids (Cnidaria: Hydrozoa) with contrasting polyp and medusa stage. *Journal of the Marine Biological Association of the U. K.* 82: 541-553.

Lindsay D., Pages F., Corbera J., Miyake H., Hunt J.C., Ichikawa T., Segawa K., Yoshida H. 2008. The anthomedusan fauna of the Japan Trench: preliminary results from in situ surveys with manned and unmanned vehicles. *Journal of the Marine Biological Association of the U. K.* 88(8): 1519-1539.

Lindsay D.J., Grossmann M.M., Bentlage B., Collins A.G., Minemizu R., Hopcroft R.R., Miyake H., Hidaka-Umetsu M., Nishikawa J. 2017. The perils of online biogeographic databases: a case study with the 'monospecific' genus *Aegina* (Cnidaria, Hydrozoa, Narcomedusae). *Marine Biology Research* 13(5): 494-512.

Lütken C. 1850. Nogle Bemaerkninger om Medusernes systematiske Inddeling, navnlig med Hensyn til Forbes's History of British Naked-eyed Medusae. *Videnskabelige meddelelser fra Dansk naturhistorik Forening* 1850: 15-35.

Maas O. 1893. Die Craspedoten Medusen der Plankton Expedition. *Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 ausgeführten Plankton-Expedition der Humboldt Stiftung* 2(Kc): 1-107.

Maas O. 1897. Die Medusen. 21st Reports on an exploration off the West Coast of Mexico, Central and South America and of the Galapagos Islands, in charge of A. Agassiz by the U.S. Fish Commission Steamer "Albatross" during 1891. *Memoirs of the Museum of Comparative Zoology at Harvard College* 23(1): 1-92, pls 1-15.

Maas O. 1905. Die Craspedoten Medusen der Siboga-Expeditie. *Siboga Expeditie* 10: 1-84, pls 1-14. DOI: 10.5962/bhl.title.11301

Maas O. 1906. Méduses d'Amboine. *Revue suisse de Zoologie* 14: 81-107.

Madin L.P., Hamner W.M., Haddock S.H.D., Matsumoto G.I. 2013. Scuba Diving in Blue Water: A Window on Ecology and Evolution in the Epipelagic Ocean. *In:* Lang M.A., Marinelli R.L., Roberts S.J., Taylor P.R. (eds). Research and

Discoveries: The Revolution of Science through Scuba. *Smithsonian Contributions to the Marine Sciences* 39: 71-82.

Madkour F., Zaghloul W., Mohammad S. 2019. First geographical Record of *Corymorpha bigelowi* (Cnidaria: Hydrozoa, Corymorphidae) in the Northern Red Sea Coast of Egypt, based on morphological description. *International Marine Science Journal* 1: 10-16.

Maggioni D., Galli P., Berumen M. L., Arrigoni R., Seveso D., Montano S. 2017. *Astrocoryne cabela*, gen. nov. et sp. nov. (Hydrozoa : Sphaerocorynidae), a new sponge-associated hydrozoan. *Invertebrate Systematics* 31: 734-746.

Maggioni D., Arrigoni R., Galli P., Berumen M. L., Seveso D., Montano S. 2018. Polyphyly of the genus *Zanclea* and family Zancleidae (Hydrozoa, Capitata) revealed by the integrative analysis of two bryozoan-associated species. *Contributions to Zoology* 87: 87-104.

Maggioni D., Schiavo A., Ostrovsky A.N., Seveso D., Galli P., Arrigoni R., Berumen M.L., Benzoni F., Montano S. 2020. Cryptic species and host specificity in the bryozoan-associated hydrozoan *Zanclea divergens* (Hydrozoa, Zancleidae). *Molecular Phylogenetics and Evolution* 151: 106893. DOI: 10.1016/j.ympev.2020.106893

Marques A.C., Maronna M.M., Collins A.G. 2013. Putting GenBank Data on the Map. *Science* 341(6152): 1341.

Martell-Hernández L.F., Sánchez-Ramírez M., Ocaña-Luna A. 2014. Distribution of planktonic cnidarian assemblages in the southern Gulf of Mexico, during autumn. *Revista Chilena de Historia Natural* 87(1): 1-11.

Mayer A.G. 1894. An account of some medusae obtained in the Bahamas. *In:* Cruise of the Steam Yacht "Wild-Duck" in the Bahamas, January to April 1893, in charge of Alexander Agassiz. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 25(11): 235-242.

Mayer A.G. 1900. Some medusae from the Tortugas, Florida. *Bulletin of the Museum of Comparative Zoology of Harvard* 37(2): 13-82, pls 1-44.

Mayer A.G. 1904. Medusae of the Bahamas. *Memoirs of Natural Sciences / Museum of the Brooklyn Institute of Arts and Sciences* 1(1): 1-33, pls 1-7.

Mayer A.G. 1910. Medusae of the world. Hydromedusae, Vols. I & II. Scyphomedusae, Vol III. Carnegie Institution, Washington, pp. 735, plates 1-76.

Mayer A.G. 1915. Medusae of the Philippines and of Torres Strait. Papers from the Department of Marine Biology of the Carnegie Institution of Washington 8: 157-202.

McCrady J. 1857. Description of *Oceania* (*Turritopsis*) *nutricula* nov. spec. and the embryological history of a singular medusan larva, found in the cavity of its bell. *Proceedings of the Elliot Society of Natural History* 1: 55-90.

McCrady J. 1859. Gymnopthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103-221, pls 8-12.

Medel M.D., Vervoort W. 2000. Atlantic Haleciidae and Campanulariidae (Hydrozoa, Cnidaria) collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, The Netherlands. *Zoologische Verhandelingen* 330: 1-68.

Menon M.G.K. 1932. The Hydromedusae of Madras. *Bulletin of the Madras Government Museum, new series, Natural History Section* 3(2): 1-32, pls 1-3.

Metschnikoff E. 1882. Vergleichend-embryologische Studien. *Zeitschrift für wissenschaftliche Zoologie* 36(3): 433-444, pl. 28. https://www.biodiversitylibrary.org/page/45332062

Metschnikoff E. 1886. Medusologische Mittheilungen. *Arbeiten des zoologischen Instituts der Universität Wien* 6: 1-30[237-266], pls 22-23. http://www.biodiversitylibrary.org/page/55122585

Miglietta M.P., Maggioni D., Matsumoto Y. 2018a. Phylogenetics and species delimitation of two Hydrozoa (phylum Cnidaria): *Turritopsis* (McCrady, 1857) and *Pennaria* (Goldfuss, 1820). *Marine Biodiversity* 49: 1085-1100.

Miglietta M.P., Piraino S., Pruski S., Alpizar Gonzalez M., Castellanos-Iglesias S., Jeronimo-Aguilar S., Lawley J.W., Maggioni D., Martell L., Matsumoto Y., Moncada A., Nagale P., Phongphattarawat S., Sheridan C., Soto Angel J.J., Sukhoputova A., Collin R. 2018b. An integrative identification guide to the Hydrozoa (Cnidaria) of Bocas del Toro, Panama. *Neotropical Biodiversity* 4(1): 102-112, and supplementry material.

Migotto A.E. 1996. Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen, Leiden* 306(23): 1-125.

Migotto A.E., De Andrade L.P. 2000. The life cycle of *Hebella furax* (Cnidaria: Hydrozoa): a link between a lafoeid hydroid and a laodiceid medusa. *Journal of natural History* 34(10): 1871-1888.

Millard N.A.H. 1957. The Hydrozoa of False Bay, South Africa. *Annals of the South African Museum* 43(4): 173-243.

Mills C.E. 1983. Vertical migration and diel activity patterns of hydromedusae: studies in a large tank. *Journal of Plankton Research* 5(5): 619-635.

Mills C.E., Pugh P.R., Harbison G.R., Haddock S.H.D. 1996. Medusae, siphonophores and ctenophores of the Alboran Sea, south western Mediterranean. *Scientia Marina* 60(1): 145-163.

Montano S., Maggioni D., Arrigoni R., Seveso D., Puce S., Galli P. 2015. The Hidden Diversity of *Zanclea* Associated with Scleractinians Revealed by Molecular Data. *PLoS ONE* 10(7) DOI: 10.1371/journal.pone.0133084

Montano S., Maggioni D., Galli P., Hoeksema B.W. 2017. A cryptic species in the *Pteroclava krempfi* species complex (Hydrozoa, Cladocorynidae) revealed in the Caribbean. *Marine Biodiversity* 47(1): 83-89.

Moura C.J., Harris D.J., Cunha M.R., Rogers A.D. 2008. DNA barcoding reveals cryptic diversity in marine hydroids (Cnidaria, Hydrozoa) from coastal and deep-sea environments. *Zoologica Scripta* 37(1): 93-108.

Müller J. 1851. Über eine eigenthümliche Meduse des Mittelmeeres und ihren Jugendzustand. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin* 1851: 272-277, pl. 11.

Müller F. 1861a. *Cunina Köllikeri* n. sp. Beitrag zur naturgeschichte der Aeginiden. *Archiv für Naturgeschichte* 27(1): 42-52.

Müller F. 1861b. Polypen und Quallen von Santa Catharina. *Olindias sambaquiensis*, n.sp. *Archiv für Naturgeschichte* 27: 312-319, pl. 9.

Nagata R.M., Nogueira Junior M., Haddad M.A. 2014. Faunistic survey of Hydromedusae (Cnidaria, Medusozoa) from the coast of Parana State, Southern Brazil. *Zootaxa* 3768(3): 291-326.

Nair K.K. 1951. Medusae of the Trivandrum Coast. Part I. Systematics. *Bulletin of the Research Institute of the University of Travancore* 20(1): 47-75, pl. 1.

Naumov D. 1960. See: Naumov D.V. 1969. Hydroids and Hydromedusae of the USSR. *Israel Program for scientific translation, Jerusalem,* pp. 463, 30 plates.

Navas D. 1971. New records of hydromedusae from the Indian Ocean. *Contribuições Avulsas do Instituto de Oceanografia da Universidade de São Paulo, Oceanografia Biológica* 22: 1-33.

Navas-Pereira D. 1980. Hydromedusae of the Bay of Sepetiba (Rio de Janeiro, Brazil). *Revista Brasileira de Biologia* 40: 817-824.

Navas-Pereira D., Vannucci M. 1991. The Hydromedusae and water masses of the Indian Ocean. *Boletim do Instituto Oceanográfico* 39(1): 25-60.

Neppi V., Stiasny G. 1912. Nachtrag zu unsrer Mitteilung: Die Hydromedusen des Golfes von Triest. *Zoologischer Anzeiger* 39(17-18): 556-557.

Neppi V., Stiasny G. 1913. Die Hydromedusen des Golfes von Triest. *Arbeiten aus dem Zoologischen Instituten der Universität Wien und der Zoologischen Station in Tries* 20(1): 1-70 [23-93], pls 1-4.

Nogueira jun. M. 2012. Gelatinous zooplankton fauna (Cnidaria, Ctenophora and Thaliacea) from Baia da Babitonga (southern Brazil). *Zootaxa* 3398: 1-21.
DOI: 10.11646/zootaxa.3398.1.1

Nogueira jun. M., Brandini F.P., Haddad M.A. 2016. First record of the hydromedusa *Aequorea macrodactyla* (Leptothecata: Aequoreidae) in Brazilian waters. *Marine Biodiversity* 46(3): 737-742.
DOI: 10.1007/s12526-015-0421-x

Nonaka A., Milisen J.W., Mundy B.C., Johnson G.D. 2021. Blackwater Diving: An Exciting Window Into the Planktonic Arena and Its Potential to Enhance the Quality of Larval Fish Collections. *Ichthyology & Herpetology* 109(1): 138-156.

Oliveira O.M.P., *et al.*. 2016. Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. *Zootaxa* 4194(1): 1-256. DOI: 10.11646/zootaxa.4194.1.1

Pagès F., Gili J.M., Bouillon J. 1992. Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (southeastern Atlantic). *Scientia Marina* 56 (Suppl. 1): 1-64.

Pagès F., Flood P. Youngbluth M. 2006. Gelatinous zooplankton net-collected in the Gulf of Maine and adjacent submarine canyons: new species, new family (Jeanbouilloniidae), taxonomic remarks and some parasites. *Scientia Marina* 70: 363-379.

Pantos O., Bythell J.C. 2010. A novel reef coral symbiosis. *Coral Reefs* 29(3): 761-770.

Patry W., Knowles T., Christianson L., Howard M. 2014. The hydroid and early medusa stage of *Olindias formosus* (Cnidaria, Hydrozoa, Limnomedusae). *Journal of the Marine Biological Association of the U. K.* 94(7): 1409-1415.

Peña Cantero A.L., Garcia Carrascosa A.M. 2002. The benthic hydroid fauna of the Chafarinas Islands (Alboran Sea, western Mediterranean). *Zoologische Verhandelingen* 337: 1-180.

Perkins H. 1906. Preliminary report. *Year book / Carnegie Institution of Washington* 4: 118.

Péron F., Lesueur C.A. 1810. Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. *Annales du Muséum national d'histoire naturelle de Paris* 14: 325-366.
https://biodiversitylibrary.org/page/3498981

Petersen K.W. 1990. Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). *Zoological Journal of the Linnean Society* 100(2): 101-231.

Pica D., Bastari A., Vaga C. F., Di Camillo C.G., Montano S., Puce S. 2017. Hydroid diversity of Eilat Bay with the description of a new *Zanclea* species. *Marine Biology Research* 13: 469-479.

Postaire B., Gelin P., Bruggemann J.H., Magalon H. 2017. One species for one island? Unexpected diversity and weak connectivity in a widely distributed tropical hydrozoan. *Heredity* 118(4): 385-394.

Prévot E. 1959. Morphologie et évolution des structures tentaculaires chez les hydraires gymnoblastes capitata. *Recueil des Travaux de la station marine d'Endoume* 29(17): 91-128.

Pruski S., Miglietta M.P. 2019. Fluctuation and diversity of Hydromedusae (Hydrozoa, Cnidaria) in a highly productive region of the Gulf of Mexico inferred from high frequency plankton sampling. *PeerJ* 7: e7848.
DOI: 10.7717/peerj.7848

Puce S., Cerrano C., Boyer M., Ferretti C., Bavestrello G. 2002. *Zanclea* (Cnidaria: Hydrozoa) species from Bunaken Marine Park (Sulawesi Sea, Indonesia). *Journal of the Marine Biological Association of the U. K.* 82(6): 943-954.

Puce S., Di Camillo C.G., Bavestrello G. 2008. Hydroids symbiotic with octocorals from the Sulawesi Sea, Indonesia. *Journal of the Marine Biological Association of the U. K.* 88(8): 1643-1654.

Purcell J.E. 2018. Successes and challenges in jellyfish ecology: examples from *Aequorea* spp. *Marine Ecology Progress Series* 591: 7-27.

Quoy J.R.C., Gaimard J.P. 1824. Voyage autour du monde... exécuté sur les corvettes de S.M. l'Uranie et la Physicienne, pendant les années 1817 à 1820. Volume 3. *In:* Freycinet, 1824. Zoologie: iv + 712 pp.

Quoy J. R. C. Gaimard J. P. 1827. Observations zoologiques faites à bord de l'Astrolabe, en mai 1826, dans le Détroit de Gibraltar. *Annales des Sciences naturelles* 10: 5-21, 172-193, 225-239.

Quoy J.R.C., Gaimard J.P. 1833. Zoologie. Voyage de la corvette l'Astrolabe : exécuté par ordre du roi, pendant les années 1826-1827-1828-1829 / sous le commandement de J. Dumont d'Urville. Volume 4, pp. 1-390. *J. Tastu, Paris.*
DOI: 10.5962/bhl.title.2132

Rajan C.T. 1963. On the larval stages of *Solmundella bitentaculata* Browne. *Journal of the Marine Biological Association of India* 5(2): 314-316.

Ranson G. 1949. Méduses. *In:* Résultats scientifiques des croisières du Navire école belge "Mercator", IV. *Memoirs of the Royal Institute of Natural Sciences of Belgium : second series.* 33: 121-158.

Raskoff K.A., Sommer F.A., Hamner W.M., Cross K.M. 2003. Collection and culture techniques for gelatinous zooplankton. *Biological Bulletin* 204(1): 68-80.

Raskoff K.A., Purcell J.E., Hopcroft R.R. 2005. Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. *Polar Biology* 28: 207-217.

Rees W.J. 1962. Hydroids of the family Cytaeidae L. Agassiz, 1862. *Bulletin of the British Museum (Natural History). Zoology series* 8: 381-400.

Russell F.S. 1940. On the nematocysts of Hydromedusae III. *Journal of the Marine Biological Association of the U. K.* 24: 515-523.

Russell F.S. 1953. The medusae of the British Isles. *Cambridge University Press, London*, 530 pp., 35 pls.

Sars M. 1835. Beskrivelser og jagttagelser over nogle mærkelige eller nye i havet ved den Bergenske kyst levende dyr af polypernes, acalephernes, radiaternes, annelidernes og molluskernes classer, med en kort oversigt over de hidtil af forfatteren sammesteds fundne ar. *T. Hallager, Bergen*. xii+81 pp.

Sassaman C., Rees J.T. 1978. The life cycle of *Corymorpha* (=*Euphysora*) *bigelowi* (Maas, 1905) and its significance in the systematics of corymorphid hydromedusae. *Biological Bulletin* 154: 485-496.

Schmidt H.E. 1973. Die Hydromedusen (Hydrozoa: Coelenterata) des Roten Meeres und seiner angrenzenden Gebiete. *Meteor Forschungs Ergebnisse* 15: 1-35.

Schmidt H.-E., Klinker J. 1974. Hydromedusae (Coelenterata) from the Indian Ocean. *Meteor Forschungsergebnisse* 18: 29-38.

Schuchert P. 1996. The marine fauna of New Zealand: athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute Memoir* 106: 1-159.

Schuchert P. 2003. Hydroids (Cnidaria, Hydrozoa) of the Danish expedition to the Kei Islands. *Steenstrupia* 27(2): 137-256.

Schuchert P. 2004. Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. *Revue suisse de Zoologie* 111(2): 315-369.

Schuchert P. 2007. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 2. *Revue suisse de Zoologie* 114(2): 195-396.

Schuchert P. 2009. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 5. *Revue suisse de Zoologie* 116(3-4): 441-507.

Schuchert P. 2010. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata part 2. *Revue suisse de Zoologie* 117(3): 337-555.

Schuchert P. 2014. High genetic diversity in the hydroid *Plumularia setacea*: A multitude of cryptic species or extensive population subdivision? *Molecular Phylogenetics and Evolution* 76: 1-9. DOI: 10.1016/j.ympev.2014.02.020

Schuchert P. 2016. The polyps of *Oceania armata* identified by DNA barcoding (Cnidaria, Hydrozoa). *Zootaxa* 4175(6): 539-555.

Schuchert P. 2017a. Systematic notes on some leptomedusa species with a description of *Neotima galeai* n. spec. (Hydrozoa, Cnidaria). *Revue suisse de Zoologie* 124(2): 351-375.

Schuchert P. 2017b. Specimen photos of DNA sample MHNG Hydrozoa DNA884. *Zenodo*. DOI: 10.5281/zenodo.998731

Schuchert P. 2018. DNA barcoding of some Pandeidae species (Cnidaria, Hydrozoa, Anthoathecata). *Revue suisse de Zoologie* 125(1): 101-127.

Schuchert P. 2019. The hydroid of the medusa *Lizzia blondina* Forbes, 1848. *Marine Biodiversity* 49: 1683-1693. DOI: 10.1007/s12526-019-00936-0

Schuchert P. 2020. World Hydrozoa Database. Accessed at http://www.marinespecies.org/hydrozoa on 2020-DEC-11. DOI: 10.14284/357

Schuchert P., Hosia A., Leclere L. 2017. Identification of the polyp stage of three leptomedusa species using DNA barcoding. *Revue suisse de Zoologie* 124: 167-182.

Segura-Puertas L. 1984. Morfología, sistemática y zoogeografía de las medusas (Cnidaria, Hydrozoa y Scyphozoa) del Pacífico Trópical Oriental. *Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Publicación Especial* 8: 1-320.

Segura-Puertas L., Suarez Morales E., Celis L. 2003. A checklist of the medusae (Hydrozoa, Scyphozoa and Cubozoa) of Mexico. *Zootaxa* 194: 1-15.

Segura-Puertas L., Celis L., Chiaverano L. 2009. Medusozoans (Cnidaria: Cubozoa, Scyphozoa and Hydrozoa) of The Gulf of Mexico (pp. 369-379). *In:* Felder D.L, Camp D.K. (eds), Gulf of Mexico – Origins, Waters, and Biota. Biodiversity. vol. 1. *Texas A&M University Press, College Station, Texas.*

Spalding M.D., Fox H.E., Allen G.R., Davidson N., Ferdaña Z.A., Finlayson M., Halpern B.S., Martin K.D., Mcmanus E., Molnar J., Recchia C.A., Robertson J. 2007. Marine Ecoregions of the World: a bioregionalization of coast and shelf areas. *BioScience* 57: 573-583.

Stampar S.N., Kodja G. 2007. Cnidaria, Hydrozoa, Anthoathecata, Pandeidae, *Stomotoca atra*: distribution extension. *Check List* 3(1): 55-57.

Stechow E. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 42(1): 1-172.

Stephens L., Calder D. 2006. Seafaring Scientist: Alfred Goldsborough Mayer, Pioneer in Marine Biology. *University of South Carolina Press,* 220 pp.

Stiasny G. 1928. Hydromedusen aus der Java-See. *Zoologische Mededelingen, Leiden* 11: 206-225.

Stretch J.J., King J.M. 1980. Direct fission: an undescribed reproductive method in Hydromedusae. *Bulletin of Marine Science* 30: 522-526.

Suehiro T., Kubota S. 2015. 166 days growth and aging of *Pandeopsis ikarii* (Uchida) (Cnidaria, Hydrozoa, Anthomedusae) appeared in the tank and new possibility of the distribution. *Kuroshio Biosphere* 11: 73-81, pl. 1.

Thiel M.E. 1936. Systematische Studien an den Trachylinae der Meteorexpedition, zugleich ein Beitrag zu einer Revision der Trachylinae. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 69: 1-92.

Thiel M.E. 1938. Die Leptolinae der "Meteor" Expedition in systematischer Betrachtung (I. Anthomedusae). *Zoologischer Anzeiger* 121: 289-303.

Thornely L.R. 1900. The Hydroid Zoophytes collected by Dr Willey in Southern Seas. *In:* Willey A. (ed.), Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896, and 1897. *Cambridge,* vol. 4, pp. 451-458, pl. 44.

Toda R., Lindsay D.J., Fuentes V.L., Moteki M. 2008. Community structure of pelagic cnidarians off Adélie Land, East Antarctica, during austral summer 2008. *Polar Biology* 37(2): 269-289.

Tosetto E., Leitao S., Nogueira jun. M. 2018. New records of *Pegantha* spp. (Hydrozoa: Narcomedusae) off Northern Brazil. *Papeis Avulsos de Zoologia* 58: e20185849. DOI: 10.11606/1807-0205/2018.58.49

Toshino S., Tanimoto M., Minemizu R. 2019. *Olindias deigo* sp. nov., a new species (Hydrozoa, Trachylinae, Limnomedusae) from the Ryukyu Archipelago, southern Japan. *ZooKeys* 900: 1-21.

Uchida T. 1927a. Studies on Japanese hydromedusae. I. Anthomedusae. *Journal of the Faculty of Science, Imperial*

University of Tokyo, Section IV, Zoology 1(3): 145-241, plates 10-11.

Uchida T. 1927b. Description of a new Leptomedusa, *Staurodiscoides gotoi*. *Japanese Journal of Zoology* 1(5): 165-168.

Uchida T. 1940. The Fauna of Akkesi Bay. XI. Medusae. *Journal of the Faculty of Science, Hokkaido Imperial University Series VI. Zoology* 7(3): 277-297.

Uchida T. 1947. Some medusae from the Central Pacific. *Journal of the Faculty of Science, Imperial University of Tokyo, Zoology* 7(3): 297-319.

Uchida T., Sugiura Y. 1975. On the formation of medusa buds in *Proboscidactyla ornata*. *Publications of the Seto Marine Biological Laboratory* 22(5): 347-354.

Uribe-Palomino J., Pausina S., Gershwin L.-A. 2018. Two new species of Hydromedusae from Queensland, Australia (Hydrozoa, Leptothecata). *ZooKeys* 783: 17-36.

Van Der Spoel S., Bleeker J. 1988. Medusae from the Banda Sea and Aru Sea plankton, collected during the Snellius II expeditions, 1984-1985. *Indo Malayan Zoology* 5: 161-202.

Vanhöffen E. 1902. Die Craspedoten Medusen der deutschen Tiefsee Expedition 1898-1899. I. Trachymedusen. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition "Valdivia"* 3: 55-86, pls 1-12.

Vanhöffen E. 1911. Die Anthomedusen und Leptomedusen der Deutschen Tiefsee Expedition 1898-1899. *Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition Valdivia* 19(5): 193-233.

Vanhöffen E. 1912. Die craspedoten Medusaen der Deutschen Südpolar-Expedition 1901-1903. *Deutsche Suedpolar Expedition* 13(Zoologie V): 353-395.

Vanhöffen E. 1913a. Ueber Westindische Medusen. *Zoologische Jahrbücher, Supplement* 11(3): 413-432.

Vanhöffen E. 1913b. Die Craspedoten Medusen der "Vettor Pisani". *Zoologica, Stuttart* 26(67): 1-34.

Vannucci M., Santhakumari V. 1969. New records of hydromedusae from the shelf area off the Kerala coast. *Journal of the Marine Biological Association of India* 11(1-2): 40-43.

Varela C. 2012. Registros nuevos de hidrozoos (Cnidaria: Hydroidomedusae) para Cuba, con la descripción de una especie nueva. *Solenodon* 10: 1-7.

von Lendenfeld R. 1885. Addenda to the the Australian Hydromedusae. *Proceedings of the Linnean Society of New South Wales* 9: 908-924, 984-985, pls 40-43.

Wang C., Huang J., Xiang P., Wang Y., Xu Z., Guo D., Lin M. 2014. Hydromedusae from the Arctic in 2010 during the 4th Chinese National Arctic Research Expedition (CHINARE 4). *Acta Oceanologica Sinica* 33(6): 95-102.

Wang C., Xu Z., Huang J., Guo D., Lin M., Xia Z. 2016. Taxonomic notes on Hydroidomedusae (Cnidaria) from South China Sea Ill: Family Rathkeidae and Zancleopsidae. *Zoological Systematics* 41(4): 392-403.

Wang C., Xu Z., Guo D., Huang J., Lin M. 2018. Taxonomic notes on Hydroidomedusae (Cnidaria) from the South China Sea V: Families Laodiceidae, Lovenellidae, Malagazziidae, and Mitrocomidae (Leptomedusae). *Acta Oceanologica Sinica* 37(10): 104-111.

Wang X., Lin K., Xu Z., Guo D., Huang J. 2019. Some new Hydroidomedusa (Cnidaria) from the northern South China Sea. *Zoological Systematics* 44(3): 191-205.

Wedler E., Larson R. 1986. Athecate hydroids from Puerto Rico and the Virgin Islands. *Studies on Neotropical Fauna and Environment* 21(1-2): 69-101.

Weill R. 1936. Existence de larves polypoïdes dans le cycle de la Trachyméduse *Olindias phosphorica* Della Chiaje. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris* 203: 1018-1020.

Werner B. 1965. Lebensgeschichte und Ökologie tropischer Hydroid- und Scyphopolypen. *Jahresbericht / Biologische Anstalt Helgoland* 1964: Ca10-Ca13.

Werner B. 1984. 4. Stamm Cnidaria, Nesseltiere (pp. 10-305). *In:* Gruner H.E. (ed.), Wirbellose Tiere. *Gustav Fischer, Stuttgart.*

Whiteaves J.F. 1901. Catalogue of the marine Invertebrata of Eastern Canada. *Geological Survey of Canada* 772: 1-272.

Woodstock M.S., Golightly C., Fenolio D., Moore J.A. 2019. *Larsonia pterophylla* (Cnidaria, Pandeidae) Parasitic on Two Leptocephali: *Paraconger* sp. (Congridae) and *Callechelyini* gen. sp. (Ophichthidae) in the Gulf of Mexico. *Gulf and Caribbean Research* 3 (1): SC7-SC10. DOI: 10.18785/gcr.3001.05

WoRMS Editorial Board 2021. World Register of Marine Species. Available from http: //www.marinespecies.org at VLIZ. Accessed 26 April 2021.

Wrobel D., Mills C. 1998. Pacific Coast Pelagic Invertebrates. A. Guide to the Common Gelatinous Animals. *Monterey Bay Aquarium, Monterey, California*, 108 pp.

Xu Z. 1983. On a new genus and species of Leptomedusae from the northern part of the South China Sea. *Acta Zootaxonomica Sinica* 8: 4-6.

Xu Z.Z., Huang J.Q. 1994. A new genus and two new species of Hydroidomedusae from Taiwan Strait. *Journal Xiamen University (Natural Science)* 33(Suppl.): 149-153.

Xu Z.Z., Huang J.Q. 2003. On new species and records of *Euphysora* in Taiwan Strait and its adjacent waters (Cnidaria, Hydrozoa, Hydroidomedusa, Anthomedusae, Capitata, Corymorphidae). *Journal of Oceanography in Taiwan Strait* 22(2): 136-144.

Xu Z.Z., Huang J.Q. 2004. A survey on Anthomedusae (Hydrozoa: Hydroidomedusae) from the Taiwan Strait with description of new species and new combinations. *Acta Oceanologica Sinica* 23(3): 549-562.

Xu Z.Z., Zhang J.B. 1978. On the Hydromedusae, Siphonophores and Scyphomedusae from the coast of the east Guangdong province and south Fujian province, China. *Journal of Xiamen University (Natural Science)* 4: 19-64. [in Chinese]

Xu Z.Z., Huang J.Q., Guo D.H. 2008. Six new species of Anthomedusae (Hydrozoa, Hydroidomedusae) from the Beibu Gulf, China (pp. 209-221). *In:* Symposium on Oceanography of the Beibu Gulf, *China Ocean Press, Beijing*

Xu Z.Z., Huang J.Q., Lin M., Guo D.H., Wang C.G. 2014. The superclass Hydrozoa of the Phylum Cnidaria in China. Vol. 1, pp. 1-456, vol. 2, pp. 495-945, *China Ocean Press, Bejing*. [in Chinese]

Xu Z., Huang J., Mao L., Guo D., Wang C. 2016. Taxonomic notes on Hydroidomedusae (Cnidaria) from South China Sea II: Family Bythotiaridae (Anthomedusae). *Zoological Systematics* 41(2): 149-157.

Zamponi M.O., Genzano G.N. 1989. Nuevas adiciones a la medusofauna de la region Subantarctica. 2. Trachymedusae (Coelenterata: Hydrozoa). *Neotropica* 34(91): 33-39.

Zhang J. 1999. Hydromedusae and Siphonophora in western waters of Taiwan Island during winter and spring. *Journal of Oceanography in Taiwan Strait* 18(1): 76-82.

Zheng L., Lin Y., Li S., Cao W., Xu Z., Huang J. 2009. *Aequorea taiwanensis* n. sp. (Hydrozoa, Leptomedusae) and mtCOI sequence analysis for the genus *Aequorea*. *Acta Oceanologica Sinica* 28: 109-115.

Zheng L., He J., Lin Y., Cao W., Zhang W. 2014. 16S rRNA is a better choice than COI for DNA barcoding hydrozoans in the coastal waters of China. *Acta Oceanologica Sinica* 33: 55-76.

Appendix 1

Checklist of hydromedusae species recorded or potentially present in the coastal region from Cape Hatteras to Florida and the whole Gulf of Mexico. Note that a number of these records are based on undocumented specimens, simply obtained by re-copying species list without published supporting information for the identifications like descriptions and illustrations. Doubtful species (Kramp, 1961; Schuchert, 2020) are excluded, but inclusion of a name does not mean that it is a recognizable species. Species determined only to genus level are excluded, except the ones seen is this study. The references for the taxonomic authorities can be found in Schuchert (2020).

species	this study	record source	comments
Suborder Filifera			
Family Bouganvillidae			
Bougainvillia carolinensis (McCrady, 1859)		1, 4, 5, 6, 11	
Bougainvillia frondosa Mayer, 1900		1, 4, 5, 6	
Bougainvillia muscus (Allman, 1863)		4, 5, 8, 9	
Bougainvillia niobe Mayer, 1894		1, 3, 4, 5, 11	
Bougainvillia platygaster (Haeckel, 1879)		1, 2, 3, 4, 5, 9	
Bougainvillia rugosa Clarke, 1882		11	
Bougainvillia triestina Hartlaub, 1911		8	barcode id.
Bougainvillia spec.	yes		
Koellikerina elegans (Mayer, 1900)		1, 6	
Koellikerina fasciculata (Péron & Lesueur, 1810)		8, 9	
Nemopsis bachei L. Agassiz, 1849		1, 5, 8, 11	
Thamnostoma tetrellum (Haeckel, 1879)		4, 5	
Family Bythotiaridae			
Bythotiara depressa Naumov, 1960		4, 5	
Bythotiara murrayi Günther, 1903		7	mesopelagic
Calycopsis chuni Vanhöffen, 1911		2	
Calycopsis papillata Bigelow, 1918		1	
Calycopsis simulans (Bigelow, 1909)		4, 5	
Protiaropsis anonyma (Maas, 1905)	yes	1, 3, 5	
Family Cytaeididae			
Cytaeis tetrastyla Eschscholtz, 1829	yes	3, 4, 5, 11	
Family Hydractiniidae			
Podocoryna americana (Mayer, 1910)		8	barcode id.
Podocoryna borealis (Mayer, 1900)		4	
Podocoryna carnea M. Sars, 1846		4	
Family Niobiidae			
Niobia dendrotentaculata Mayer, 1900		1, 4, 5, 6	

species	this study	record source	comments
Family Oceaniidae			
Oceania armata Kölliker, 1853		2, 4, 5	misidentifications of *T. nutricula* ?
Turritopsis dohrnii (Weismann, 1883)		8	barcode id.
Turritopsis nutricula McCrady, 1857	yes	1, 2, 3, 4, 5, 6, 9, 11	
Family Pandeidae			
Amphinema australis (Mayer, 1900)		1, 6, 11	species inquirenda ?
Amphinema dinema (Péron & Lesueur, 1810)		1, 4, 5, 6, 9, 11	
Amphinema rugosum (Mayer, 1900)		1, 4, 5, 6, 9, 11	
Amphinema turrida (Mayer, 1900)	yes	1, 2, 4, 5, 6, 11	
Cirrhitiara superba (Mayer, 1900)	yes	1, 6	
Eutiara mayeri Bigelow, 1918		1, 7	
Halitholus intermedius (Browne, 1902)		4, 5	identification doubtful
Larsonia pterophylla (Haeckel, 1879)	yes	1, 2, 4, 5, 6	
Leuckartiara gardineri Browne, 1916		4, 5	identification needs confirmation
Leuckartiara octona (Fleming, 1823)		4, 5	identification needs confirmation
Leuckartiara zacae Bigelow, 1940		4, 5	
Merga violacea (Agassiz & Mayer, 1899)	yes	1, 2, 4, 5, 6	
Pandea conica (Quoy & Gaimard, 1827)		1, 3	
Pandeopsis ikarii (Uchida, 1927)	yes		new record for Atlantic Ocean
Pandeopsis prolifera n. spec.	yes		
Stomotoca atra L. Agassiz, 1862		4, 5	misidentification of *L. pterophylla* ?
Family Proboscidactylidae			
Proboscidactyla gemmifera (Fewkes, 1882)	yes	1, 2, 4, 5, 6	older records include *P. stolonifera*
Proboscidactyla ornata (McCrady, 1859)	yes	1, 2, 4, 5, 6, 9, 11	
Family Protiaridae			
Halitiara formosa Fewkes, 1882		1, 2, 4, 5, 6, 9, 11	
Paratiara digitalis Kramp & Dumas, 1925		1	
Family Ptilocodiidae			
Thecocodium quadratum (Werner, 1965)	yes	10	
Family Rathkeidae			
Lizzia alvarinoae Segura, 1980		9	*Cytaeis* spec ?
Lizzia blondina Forbes, 1848		1, 4, 6, 11	includes *Podocoryna minuta*
Lizzia gracilis (Mayer, 1900)		1, 6	
Podocorynoides minima (Trinci, 1903)		4, 5, 6 ?, 9, 11	
Family Trichydridae			
Trichydra pudica Wright, 1857		5	
Suborder Capitata			
Family Cladonematidae			
Cladonema radiatum Dujardin, 1843		1, 4, 6	
Family Corynidae			
Codonium proliferum (Forbes, 1848)		4, 5	
Coryne eximia Allman, 1859		4	includes *C. gracilis*
Polyorchis karafutoensis Kishinouye, 1910		4, 5	implausible occurrence
Slabberia halterata Forbes, 1846		1, 4, 6	

species	this study	record source	comments
Slabberia strangulata (McCrady, 1859)		1, 6, 9, 11	
Stauridiosarsia gemmifera (Forbes, 1848)		4, 5	
Stauridiosarsia ophiogaster (Haeckel, 1879)		4, 5	
Stauridiosarsia reesi (Vannucci, 1956)		8	
Family Pennariidae			
Pennaria disticha Goldfuss, 1820		1, 6, 11	medusoid
Family Sphaerocorynidae			
Sphaerocoryne agassizii (McCrady, 1859)		1	
Euphysilla pyramidata Kramp, 1955	yes	4, 5	
Euphysilla peterseni Allwein, 1967		11	
Zancleopsis dichotoma (Mayer, 1900)	yes	1, 6, 11	includes *Z. gotoi* records
Family Zancleidae			
Zanclea costata Gegenbaur, 1857		1, 4, 5, 6	= in part *Z. mayeri* + others
Zanclea dubia Kramp, 1959		4, 5	identification ?
Zanclea mayeri n. spec.	yes		new species
Zanclea spec.	yes		
Suborder Aplanulata			
Family Corymorphidae			
Corymorpha forbesii (Mayer, 1894)	yes	1, 2, 4, 5, 6, 11	
Corymorpha gracilis (Brooks, 1883)	yes	1, 4, 5, 6, 9, 11	
Corymorpha floridana n. spec.	yes		new species
Corymorpha furcata (Kramp, 1948)		3, 4, 5	
Corymorpha nutans M. Sars, 1835		5, 8	? misidentifications
Euphysa aurata Forbes, 1848		4	identification doubtful
Family Tubulariidae			
Dicodonium floridana Mayer, 1910		1, 6	
Ectopleura minerva Mayer, 1900		1, 6	
Ectopleura dumortierii (van Beneden, 1844)		1, 8, 9, 11	
Order Leptothecata			
Family Aequoreidae			
Aequorea australis Uchida, 1947		8	
Aequorea floridana (Agassiz, 1862)		1, 4, 6	
Aequorea forskalea Péron & Lesueur, 1810		1, 11	
Aequorea globosa Eschscholtz, 1829		4, 5	
Aequorea macrodactyla (Brandt, 1835)		1, 2, 4, 5, 9, 11	uncertain identifications
Aequorea neocyanea new name	yes	6	new name
Aequorea taiwanensis Zheng *et al.*, 2009	yes		new record for Atlantic Ocean
Aequorea spec. 1	yes		
Aequorea spec. 2	yes		
Zygocanna cf. *apapillatus* Xu, Huang & Guo, 2014	yes		new record for Atlantic Ocean
Zygocanna vagans Bigelow, 1912		4, 5	
Rhacostoma atlanticum L. Agassiz, 1851		1	

species	this study	record source	comments
Family Blackfordiidae			
Blackfordia virginica Mayer, 1910		4, 5, 8	
Family Campanulariidae			
Clytia discoida (Mayer, 1900)		1, 4, 5, 9, 11	identification ?
Clytia elsaeoswaldae Stechow, 1914		8	barcode id.
Clytia folleata (McCrady, 1859)		1, 4, 5, 8, 9	
Clytia gelatinosa (Mayer, 1900)		1, 4, 6, 11	identification ?
Clytia globosa (Mayer, 1900)		1, 4, 6, 11	
Clytia gracilis (M. Sars, 1850)		8	barcode id.
Clytia hemisphaerica (Linnaeus, 1767)		9	id. ?, includes *C. languida*
Clytia linearis (Thornely, 1900)	yes		barcode id.
Clytia mccradyi (Brooks, 1888)		1, 5, 6	
Clytia simplex (Browne, 1902)		4, 5	indeterminable species ?
Clytia spec. 1	yes		
Clytia spec. 2	yes		
Gastroblasta timida Keller, 1883	yes		new record for Atlantic Ocean
Multioralis ovalis Mayer, 1900		1, 6	
Obelia bidentata Clark, 1875		8	barcode id.
Obelia dichotoma (Linnaeus, 1758)		8	barcode id.
Family Cirrholoveniidae			
Cirrholovenia tetranema Kramp, 1959		11	
Family Dipleurosomatidae			
Dichotomia cannoides Brooks, 1903		1, 4, 5	
Netotocertoides brachiatum Mayer, 1900		6	
Family Eirenidae			
Eirene gibbosa (McCrady, 1859)		1, 11	
Eirene lactea (Mayer, 1900)		1, 4, 6	
Eirene pyramidalis (Agassiz, 1862)		1, 4, 5, 6, 9, 11	
Eirene tenuis (Browne, 1905)		4	
Eutima coerulea (Agassiz, 1862)		1, 6	
Eutima gegenbauri (Haeckel, 1864a)		11	
Eutima gracilis (Forbes & Goodsir, 1853)		4, 5, 9	
Eutima mira McCrady, 1859		1, 4, 5, 6, 11	
Eutima suzannae Allwein, 1967		11	
Eutima variabilis McCrady, 1859		1, 5, 6, 11	
Eutonina scintillans (Bigelow, 1909)		4	
Helgicirrha cari (Haeckel, 1864a)		4, 11	includes *Helgicirrha schulzii*
Helgicirrha weaveri Allwein, 1967		11	
Family Hebellidae			
Melicertissa mayeri Kramp, 1959	yes	1	
Staurodiscus kellneri (Mayer, 1910)	yes	1, 6	includes *Toxorchis brooksi*
Staurodiscus luteus new species	yes		new species
Staurodiscus tetrastaurus Haeckel, 1879	yes	2, 6	

species	this study	record source	comments
Family Laodiceidae			
Laodicea brevigona Allwein, 1967		5, 11	
Laodicea minuscula Vannucci, 1957		4, 5	
Laodicea undulata (Forbes & Godsir, 1853)	yes	1, 4, 5, 6, 11	
Family Lovenellidae			
Eucheilota comata (Bigelow, 1909)		2	
Eucheilota duodecimalis A. Agassiz, 1862		1, 2, 4, 5, 6, 9, 11	
Eucheilota paradoxica Mayer, 1900		1, 4, 5, 6, 9	
Eucheilota ventricularis McCrady, 1859		1, 6, 9, 11	
Lovenella bermudensis (Fewkes, 1883)		1, 6, 11	
Family Malagazziidae			
Octophialucium aphrodite (Bigelow, 1928)	yes	1, 5	
Octophialucium irregularis n. spec.	yes		new species
Octophialucium medium Kramp, 1955		4, 5	
Malagazzia carolinae (Mayer, 1900)		1, 2, 6, 8	
Family Orchistomatidae			
Orchistoma pileus (Lesson, 1843)	yes	1, 4, 5, 6	includes *O. collapsum* and *O. agariciforme*
Family Phialellidae			
Phialella parvigastra (Mayer, 1900)		1, 6	
Family Tiarannidae			
Chromatonema rubrum Fewkes, 1882		4, 5	
Modeeria rotunda (Quoy & Gaimard, 1827)		4	
Family Tiaropsidae			
Tiaropsidium roseum (Maas, 1905)		6	
Wuvulidae new family			
Wuvula ochracea (Mayer, 1910)	yes	1, 6	
Narcomedusae			
Family Aeginidae			
Aegina citrea Eschscholtz, 1829		3, 4, 5, 9	misidentifications of *P. rhodina* ?
Aeginura grimaldii Maas, 1904		4, 5, 7	
Family Cuninidae			
Cunina becki Bouillon, 1985	Yes		new record for Atlantic Ocean
Cunina duplicata Maas, 1893		3, 5	
Cunina fowleri (Browne, 1906)		3, 4, 5	
Cunina globosa Eschscholtz, 1829		5	
Cunina octonaria McCrady, 1859	Yes	3, 4, 5, 9, 11	
Cunina peregrina Bigelow, 1909		3, 5, 11	
Solmissus incisa (Fewkes, 1886)		4, 5, 6, 7	
Solmissus marshalli Agassiz & Mayer, 1902		3, 7	
Family Pseudaeginidae			
Pseudaegina rhodina (Haeckel, 1879)	Yes	6, 7	some *A. citrea* records belong to here

species	this study	record source	comments
Family Solmarisidae			
Pegantha clara R.P. Bigelow, 1909		3, 4, 7	
Pegantha martagon Haeckel, 1879	Yes	3, 4, 5	
Pegantha polystriata (Xu & Zhang, 1978) new comb.	Yes		new record for Atlantic Ocean
Pegantha triloba Haeckel, 1879		3, 4, 5	
Solmaris corona (Keferstein & Ehlers, 1861)	Yes	3, 7	
Solmaris flavescens (Kölliker, 1853)		3, 7	
Solmaris flavofinis new spec.	Yes		new species
Family Solmundaeginidae			
Solmundella bitentaculata (Quoy & Gaimard, 1833)	Yes	3, 4, 6, 9, 11	
Order Trachymedusae			
Family Halicreatidae			
Botrynema brucei Browne, 1908		7	mesopelagic
Halicreas minimum Fewkes, 1882		4, 5, 7	
Haliscera bigelowi Kramp, 1947		5, 7	
Haliscera conica Vanhöffen, 1902		7	mesopelagic
Halitrephes maasi Bigelow, 1909		7	mesopelagic, includes *H. valdiviae*
Family Rhopalonematidae Russell, 1953			
Aglantha elata (Haeckel, 1879)		5	
Aglaura hemistoma Péron & Lesueur, 1810	Yes	3, 4, 5, 6, 9, 11	
Amphogona apicata Kramp, 1957		7	mesopelagic
Amphogona apsteini (Vanhöffen, 1902)	Yes	3, 4	
Benthocodon pedunculatus (Bigelow, 1913)		7	mesopelagic
Colobonema sericeum Vanhöffen, 1902		4, 5, 7	
Crossota rufobrunnea (Kramp, 1913)		4, 5, 7	
Pantachogon haeckeli Maas, 1893		4, 5, 7	
Persa incolorata McCrady, 1859		3, 5, 9, 11	
Rhopalonema funerarium Vanhöffen, 1902		4, 5	
Rhopalonema velatum Gegenbaur, 1857	Yes	3, 4, 5, 9, 11	
Sminthea eurygaster Gegenbaur, 1857		3, 4, 5	
Order Limnomedusae			
Family Geryoniidae			
Geryonia proboscidalis (Forsskål, 1775)	yes	3, 4, 5	
Liriope tetraphylla (Chamisso & Eysenhardt, 1821)	yes	3, 4, 5, 6, 8, 9, 11	
Family Olindiidae			
Cubaia aphrodite Mayer, 1894		1, 4, 6	
Gossea brachymera Bigelow, 1909		1, 2, 4, 5	
Olindias muelleri Haeckel, 1879		1	misidentification ?
Olindias tenuis (Fewkes, 1882)	yes	4, 6	
Scolionema suvaense (Agassiz & Mayer, 1899)		1, 2, 4	
Vallentinia gabriellae Vannucci Mendes, 1948		1, 4	

Sources:

1 Kramp (1959a): Table VII – Neritic species in the West - Atlantic tropical region Cape Hatteras to Florida

2 Kramp (1959a): Table XII – Neritic, predominantly warm water species and their distribution in the three great oceans - West Indies and N. American Warm Water

3 Kramp (1959a): Table X – Oceanic species in the epipelagic zone-Atlantic warm water - Eastern and Western, excluding strictly western Atlantic species

4 Segura-Puertas *et al.* (2003): Checklist of Medusa of Mexico

5 Segura-Puertas *et al.* (2009): Medusozoans of the Gulf of Mexico

6 Mayer (1910): Mayer collected hydrozoans extensively along the Atlantic seaboard including the Dry Tortugas from 1892 to 1900. In 1903 he established a marine station on Dry Tortugas, Florida which operated until 1939.* Washed by the Gulf Stream current, the Dry Tortugas are approximately 300 nautical miles from the sampling site and perhaps 3 to 10 days drift in Gulf Stream. We place additional emphasis on species collected by Mayer at Dry Tortugas. These entries are not from a checklist.
*Carnegie Institution of Washington Administration Records, 1890-2001, Administration, Carnegie Institution of Washington, Washington D.C.

7 Larson *et al.* (1991): Observations from submersable at Tortugas and Bahamas, surface to 900 m, observations excluded specimens less than 1 cm; New England only observations are excluded here.

8 Pruski & Miglietta (2019): identifications via 16S sequences

9 Martell-Hernández *et al.* (2014)

10 Kubota & Meldonian (2016)

11 Allwein (1967)

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Revisiting the Oriental genus *Syleter* Andrewes, 1941 (Coleoptera: Carabidae: Clivinini)

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Abstract: The species group formerly included in the genus *Syleter* Andrewes, 1941 from the Oriental region is redefined resulting in the split of three genera, the original genus *Syleter* and two new genera, *Parasyleter* gen. nov. and *Clypeuspinus* gen. nov. Genus descriptions of the three genera and an identification key to the three genera is provided. Type species for the three genera are either re-established or designated and illustrations are provided for all of them. The genus *Syleter* is revised. The species *Syleter acutipalpis* (Putzeys) is resurrected to species status from synonymy with *S. paradoxus* (Putzeys). For *S. acutipalpis* a lectotype has been designated in order to maintain nomenclatural stability. The following new taxa are described: *S. sinepunctatus sinepunctatus* sp. nov., *S. sinepunctatus kluangensis* ssp. nov., and *S. gradus* sp. nov. A key to the *Syleter* species is provided. The genus *Clypeuspinus* gen. nov. is represented by one species, *C. validus* (Andrewes) comb. nov., which is redescribed.

Keywords: Oriental region - taxononmy - *Clypeuspinus* gen. nov. - *Parasyleter* gen. nov. - new species - key to taxa - distribution.

INTRODUCTION

The genus *Syleter* Andrewes, 1941 occurs in the Oriental and Ethiopian region. It is not well represented in museum and private collections. For Oriental members, the genus was keyed out with five species by Andrewes (1927, 1929) under the name *Psilus* Putzeys, 1877. Later the genus *Psilus* was renamed *Syleter* because it was preoccupied (Andrewes, 1941). Two more species were described from Sri Lanka (Andrewes, 1936) and Papua New Guinea (Darlington, 1962).

Twenty years ago, the Oriental members were keyed out, a catalogue of the species was provided, and two groups, the *paradoxus*-species group and the *doriae*-species group, were distinguished (Balkenohl, 2001). This first approach was performed to provide some orientation on the very heterogeneous group ranging in size from 1.8 to 4.8 mm. Meanwhile, substantial material came to my attention, material from all known species but also of some undescribed species. In addition, some more type material became available. The evaluation suggested a better discrimination of the two species groups and demonstrated the necessity to split the genus *Syleter* into the two genera characterized in this contribution. Moreover, the species *C. validus* (Andrewes, 1936) was found to be so conspicuously different from all of the other species that it does not fit with the group characteristics of both genera, a misplacement already indicated earlier (Balkenohl, 2001). Above all, comparisons with members of other genera of the tribe showed that the species does not match with any genus description.

Consequently, this contribution aims to clarify the taxonomic status of the members of the group previously summarized under the name of *Syleter*.

MATERIAL AND METHODS

In general, terms, descriptions of characters, methods for mounting of inner structures, microscopy and photographs are based on Balkenohl (2001, 2021b).

For the evaluation 201 Oriental specimens including type and other material were investigated. In general, all additional informative material like original paper cards and pins have been kept at the specimens. The complete information given on the labels is quoted verbatim as it appears, including original spacing, upper case letters, and punctuation. Moreover, the data of the name bearing material is displayed in quotation marks. For the descriptions, the length was measured from the most anteriorly projecting part of the head (clypeus or clypeal wings) and does not include the elongate mandibles. The length of the pronotum was measured along the median line and includes the posteriorly elongated flange. The width of the pronotum and elytra was measured at the maximum width. The description of the genitalia refers

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to the natural position the genitalia exhibit in soaked specimens before they are extracted, cleaned, and mounted.

For the comparisons to other genera and species mentioned in the text material from the author's collection was used. Moreover, *Oxygnathus* material was loaned from the ETHZ.

Abbreviations used:

ADCW	Alexander Dostal collection (including Coll. Karel Kult), Vienna, Austria
BMNH	Natural History Museum, London, United Kingdom
MBCB	Michael Balkenohl working collection, Bonstetten, Switzerland
ETHZ	Eidgenössische Technische Hochschule Zürich, Switzerland
MFNB	Museum für Naturkunde Berlin, Germany
MHNG	Muséum d'Histoire Naturelle de Genève, Switzerland
MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMB	Naturhistorisches Museum Basel, Switzerland
NHMW	Naturhistorisches Museum, Vienna, Austria
PBCP	Petr Bulirsch Collection, Prague, Czech Republic
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
TACA	Thorsten Assmann working collection, Asendorf (part of Zoologische Staatssammlung München), Germany
[…]	in brackets: additional information by the author
$\bar{x}$	arithmetic mean (used in the measurements for the descriptive statistics)

TAXONOMY

Order Coleoptera
Family Carabidae Latreille, 1802
Subfamily Scaritinae Bonelli, 1810
Tribe Clivinini Rafinesque, 1815

Among the Oriental Clivinini, the group formerly known as *Syleter* shares the following general characters:

Head with frons, clypeus, and supraantennal plate more or less elongated, flattened or slightly convex, without median keel or carinae, laterally with two supraorbital and with one clypeal seta; mandible elongated; maxillary palp elongated, either distinctly securiform or bottle-like; antenna with pedicellus eccentrically attached to scapus. Pronotum without big groove-like punctures, without distinct sulci. Elytron with striae one to three free at the base, reflexed lateral margin and lateral channel running up to the apex, interval three without or with three setigerous punctures. Proepisternum not distinctly tumid laterally, visible or not visible in dorsal view in basal third. Ventral surface with last visible abdominal segment with the two setigerous punctures laterally widely separated. Front leg with basal tarsomere without rows of numerous setae on dorsal surface.

Genus *Syleter* Andrewes, 1941

Psilus Putzeys, 1877: XLVI. – Andrewes, 1929: 386. [invalid junior homonym of *Psilus* Panzer, 1801 (Hymenoptera)]
Syleter Andrewes, 1941: 317.

Type species: *Psilus acutipalpis* Putzeys, 1877, by monotypy; type locality: Bangkok.

Identification key to the genera formerly included in *Syleter*

1A Clypeus, wing of clypeus, and supraantennal plate fused, without notches, wing of clypeus not or only indistinctly projecting, usually projecting anteriorly at same level as clypeus (Figs 1, 2); mandible straight laterally and hooked at apex; pronotum with lateral channel of equal width between the two lateral setigerous punctures; flange at base of pronotum convex, much wider than basal constriction; elytron with interval eight convex; mesotibia without or with small seta furnished tubercle preapically (Figs 4, 5) 2

1B Clypeus, wing of clypeus, and supraantennal plate separated by obtuse notch, wing of clypeus distinctly projecting anteriorly (Fig. 3); mandible convex laterally and regularly arcuate in apical half, bend slightly dorsally; pronotum with lateral channel distinctly widened between the two lateral setigerous punctures; flange at base of pronotum carinate, as wide as basal constriction; elytron with interval eight carinate from humerus to apex; mesotibia with long spine-like protuberance preapically furnished with seta (Fig. 6) ..... ***Clypeuspinus* gen. nov.**

2A Reflexed lateral margin of pronotum reaching from anterior angle to basal constriction, posterior angle marked by a tooth or a knob-like thickening, median line distinctly joining with basal constriction; pronotum distinctly trapezoid; interval three of elytron with three setigerous punctures; mesotibia with small protuberance preapically; mentum elongated, with acute lobe; female genitalia with coxostylus one and two not completely fused ..... ***Syleter* Andrewes, 1941**

2B Reflexed lateral margin shortened, reaching from anterior angle to posterior setigerous puncture, posterior angle missing, median line not or very indistinctly joining basal constriction; pronotum square or indistinctly trapezoid; interval three of elytron without setigerous punctures; mesotibia without tubercle preapically; mentum not elongated, lobe short and convex; female genitalia with coxostylus one and two completely fused ..... ***Parasyleter* gen. nov.**

Genus diagnosis: *Size* 2.8 to 4.5 mm. *Head* with clypeus and frons conspicuously elongated and flattened anteriorly; clypeus, clypeal wing, and supraantennal plate fused; clypeus straight or slightly convex anteriorly, projecting as far as clypeal wing; mandible distinctly elongated, narrow in apical half, laterally straight, hooked at apical tip; labrum three- or seven-setose; maxillary palpomere extraordinarily narrowed and slender in apical half, gently curved concavely outwards, the two apical segments longitudinally securiform; antenna with scapus and pedicellus eccentrically attached; eye not reduced. Mentum distinctly elongated, with lateral lobe acutely projecting, median tooth wide, truncated, not projecting as far as lateral lobe, surface with rough meshes. *Pronotum* distinctly trapezoid, with reflexed lateral margin complete, running from anterior angle up to basal constriction, posterior angle with obtuse small tooth which is crossing the lateral channel and pointing anteriorly, lateral channel of equal width, median line distinct, joining and engraved up to basal constriction; proepisternum invisible in dorsal view; flange at base convex, two to four times as wide as basal constriction. *Elytron* with interval eight convex, lateral channel slightly flared apically, with interval eight not or slightly emarginated and row of umbilical setigerous punctures indistinctly following the emargination, interval eight at apex convex or with emarginated carina; with row of umbilical setigerous punctures apically slightly oriented to interval eight; third interval with three

Identification key to the species of the genus *Syleter*

1A Labrum 3-setose; pronotum without reticulation and punctures on disk, with posterior angle rounded off; elytron with all intervals smooth, without tubercle at declivity of third interval, striae narrow, with punctures distinct, umbilical setigerous punctures with wider distance at middle; aedeagus at apex spoon-like widened, parameres with four setae each. Body length 2.8 mm. Borneo (central and southeast) ..... ***S. fulvaster***

1B Labrum 7-setose; pronotum with reticulation and with or without punctures on disk, with posterior angle more or less marked; elytron with all or with interval eight reticulated, with tubercle at declivity of third interval, striae wide, finely crenulated, with punctures indistinct, umbilical setigerous punctures of equal distance; aedeagus at apex securiform widened or spatulate, parameres without or with two setae each 2

2A Head anterior eye-level moderately elongated; neck constriction complete and developed as sharp angular step with level distinctly higher than neck; lateral channel of pronotum from posterior angle to base distinctly widened; apex of aedeagus developed as acute spatula, parameres with two setae each. Body length 3.61-3.64 mm. Myanmar .. .. ***S. acutipalpis***

2B Head anterior eyes conspicuously elongated; neck constriction incomplete and developed as row of punctures, with a more or less wide gap at middle and with posterior part of frons at middle as high as neck or developed as rounded step and complete; lateral channel of pronotum from posterior angle to base narrow 3

3A Disk of pronotum without punctures; anterior margin of labrum straight; supraorbital plate covered with distinct longitudinal reticulation; interval eight of elytron with more or less distinct reticulation; apex of aedeagus developed as wide spatula. Body length 3.37-3.8 mm. Borneo ..... ***S. sinepunctatus sinepunctatus* sp. nov.**

- Specimen from West Malaysia: Lateral margin of elytron convex with maximum width at middle; intervals five to seven of elytron with indistinct reticulation; apex of aedeagus acutely pointed at tip and turns to a different direction as in the nominotypical subspecies. Body length 3.45 mm. Jahore, Kluang ..... ***S. sinepunctatus kluangensis* ssp. nov.**

3B Disk of pronotum with punctures; anterior margin of labrum convex; supraorbital plate smooth; interval eight of elytron or all intervals with reticulation; apex of aedeagus developed either as narrow acuminated spatula or securiform 4

4A Disk of pronotum laterally with few single punctures in the basal part; anterior margin of pronotum distinctly excised, anterior angle projecting; apex of aedeagus developed as narrow acuminated spatula; Body length 3.32-3.6 mm. New Guinea and Papua-New Guinea, Northeast Australia (Queensland): Cape York ..... ***S. papua***

4B Disk of pronotum with numerous punctures arranged laterally as paramedian and paralateral group; anterior margin of pronotum straight, anterior angle not projecting; apex of aedeagus securiform 5

5A All intervals of elytron longitudinally reticulated; pronotum with paramedian and paralateral band of punctures extending from anterior fifth to basal declivity; neck constriction complete and developed as rounded step; apex of aedeagus broadly securiform, stout. Body length 4.25-4.66 mm. Borneo ..... ***S. gradus* sp. nov.**

5B Interval eight of elytron longitudinally reticulated (in some cases also interval seven); pronotum with more or less circular paramedian and paralateral group of punctures restricted to basal half; neck constriction incomplete and developed as lateral punctures with more or less wide gap in between; apex of aedeagus long securiform. Body length 3.51-4.32 mm. Hong Kong, Thailand, Cambodia, Vietnam (South), Malaysia, Singapore .... ***S. paradoxus*** (= *S. trapezicollis*)

setigerous punctures. *Hind wings* fully developed. *Legs* in both sexes with front tarsomeres distinctly widened, intermediate tarsomeres moderately widened; widening in males more distinct and ventrally with small whitish setae; mesotibia with four setae laterally, preapical seta arising from small protuberance (Fig. 4). *Male genitalia* with aedeagus conspicuously curved, apical part elongated, apex more or less spatulate or securiform; parameres conspicuously asymmetric. *Female genitalia* with coxostylus one and two not completely fused, with cone-like seta in apical quarter.

Differential diagnosis: See key to the genera.

Syleter paradoxus (Putzeys, 1868)

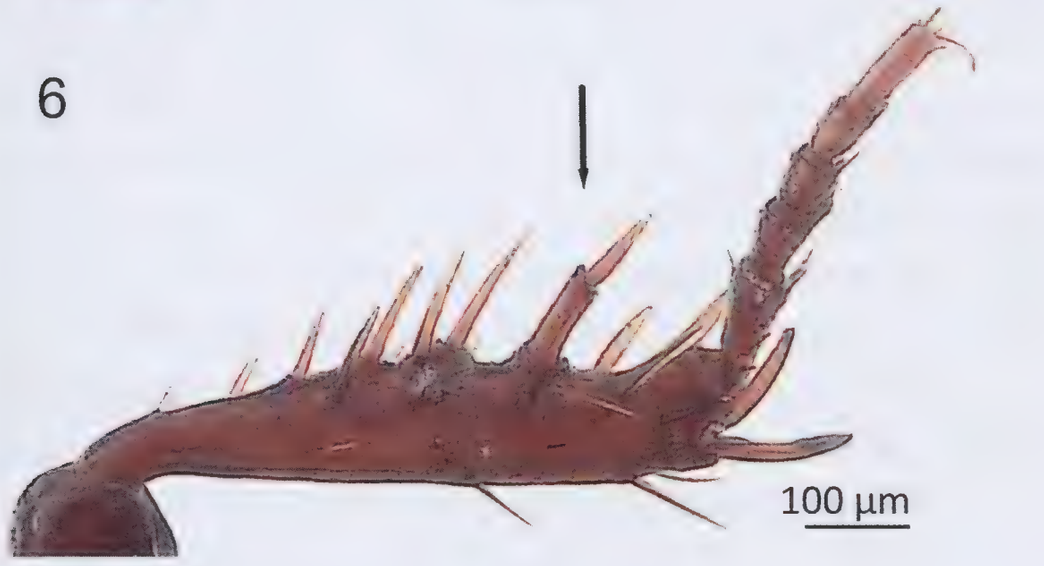
Figs 1, 4, 7, 14, 21

Ardistomis paradoxa Putzeys, 1868: 21.
Clivina trapezicollis Bates, 1889: 263.
Psilus paradoxus. – Andrewes, 1926: 381. – Andrewes, 1927: 266. – Andrewes, 1929: 387, fig. 58. – Andrewes, 1930: 288.
Syleter paradoxus. – Lorenz, 1998: 138. – Balkenohl, 2001: 30, fig. 39. – Aston, 2016: 215. – Lorenz, 2005: 148. – Balkenohl, 2017: 260.

Type material examined: Holotype of *Syleter trapezicollis* (Bates, 1889): MNHN; with labels and data: white, handwritten in black ink "Conchin China" / white, handwritten in black ink "Clivina trapezicollis Bates" / red, printed "TYPE".

Additional material: HONG KONG. MBCB; 1 ♀, H.K. Wu Kau Tang, moss/stream, leg. P. Aston, 7.II.13. – LAOS. NHMW; 1 ♀, N-Laos: Prov. Lg. Nam Tha Luang Nam Tha, at light 19.6.1996, 550 m leg. Schillhammer. – PBCP; 1 spec., Laos c. Kammouan prov. Nam Theun env., alt. 500 m Route No 8, N 17°50.7' E 105°03.2', 2.-4.5.1998, E. Jendek, O. Sauša lgt. – CHINA. Specimens from Yunnan were investigated in 2001 by the author. – THAILAND. MBCB; 1 ♀, Thailand, Changwat, Chiang Mai, Chiang Mai, 250 m, 15.1.1989, leg. Trautner & Geigenmüller. – MFNB; 1 ♀, NO-Thailand, Khon Kaen, lux, 23.11.1989, leg. S. Saowakontha. – TACA; 1 ♀, Thailand, Bangkok, light trap, IX.8.52, W.E. Griffith. – NHMW; 2 ♂♂, 2 ♀♀, S-Thailand, Tale Noi, 7°47'N 100°13'E, Licht, 1.-2.5.1993, leg. Malicky. – MBCB; 1 ♀, 3 specimens, S Thailand, Sai Buri, Pattani dist., 23.-28.4.1993, J. Strnad leg. – ADCW; 1 ♂, 1 ♀, same data. – PBCP; 10 specimens, same data but 25.IV.1993. – ADCW; 1 ♂, 1 ♀, 2 specimens, same data but J. Horák leg. – CAMBODIA. RBINS; 1 ♂, Coll. I.R.Sc.N.B., Cambodia, Banteay Meanchey prov., Ang Trapeang Thmor, Malaise trap, 15.vi.2006, leg. loc ranger. – RBINS; 2 ♀♀, Coll. I.R.Sc.N.B., Cambodia Banteay M prov., Ang Trapeang Thmor W.S. Light Trap, Office Int. Crane F., 18.VI.2005, leg Var & Hagebaert. – NHMB; 1 spec., Indo Chine, Coll. Dussault, Battambang, 1913. – PBCP; 1 spec., Cambodia mer., Takfu, 5.V.84, leg. Frühbauer. – VIETNAM (SOUTH). BMNH; 1 ♀, Saigon, H.E.Andrewes Coll. B.M. 1945-97, figured specimen, Psilus paradoxus Putz. compared with type H.E.A. – MNHN; 1 spec., Saigon, 12.1926, Muséum Paris J. Duchaine 1928. – MNHN; 4 specimens [one of them without pronotum], same data but Coll. A. Bonhoure, 1909. – NHMW; 1 ♂, 3 ♀♀, 31 specimens, S-Vietnam, Nam Cat Tien Nat. Park, 1.-15.5.1994,

Figs 1-3. Head, dorsal view. (1) *Syleter paradoxus* (Putzeys, 1868). (2) *Parasyleter doriae* (Putzeys, 1873) comb. nov. (3) *Clypeuspinus validus* (Andrewes, 1936) comb. nov.



Figs 4-6. Right mesotibia. (4) *Syleter paradoxus* (Putzeys, 1868) showing the small preapical protuberance and its seta inserted apically (arrow). (5) *Parasyleter doriae* (Putzeys, 1873) comb. nov. with no tubercles at all. (6) *Clypeuspinus validus* (Andrewes, 1936) comb. nov. showing the long protuberance and its seta inserted laterally (arrow).

Pacholatko & Dembicky. – MNHN; 2 specimens, Vinh-Long, Nov 77, Vinh long Draubert, Muséum Paris ex Coll. R. Oberthür 1952. – MBCB; 1 spec., Vinh-Long, Lumiere Coch, I 48. – PBCP; 1 spec., Long Thanh. – NHMW; 3 specimens, S-Vietnam, 40 km NW An Khe Buon Luoi, 620-750 m, 14°10'N 108°30'E 28.3, 12.4.1995, Pacholatko & Dembicky. – MNHN; 2 specimens, Conchin China, Psilus trapezicollis [one of them found with empty abdomen]. – BMNH; 1 ♀, 3 specimens, Conchinchine, Bien Hoa, 12-1902, Cap. Fouquet, Psilus trapezicollis Bates, Museum Paris ex Coll. M. Maindron Coll. G. Babault 1930, one of them with additional label = Psilus paradoxus Putz. det. Kult. – BMNH; 1 ♀, Conchinchine, Long Xuyen, Dorr., Ex. Coll. E. Fleutiaux, Psilus trapezicollis Bates compared with type H.E.A., H.E. Andrewes Coll. B.M. 1945-97. – MALAYSIA. – BMNH; 1 ♂, Malaya, Kuan, at light, 28.XII.1926, G.H. Corbett., Gesch. 8.1938 von Andrewes, ex. coll. Brit. Mus., 3017, paradoxus Putz., F. van Emden Bequest. B.M. 1960129, Psilus paradoxus Putz. H.E.Andrewes det.; – NHMG; 1 ♂, Malaisie, Selangor, Sungei Buloh, Kuala Lumpur, 27-VII-72, T. Jaccoud; – BMNH; 1 ♀, Penang, Bowring 63.47*, Psilus paradoxus Putz. (over), compared with type H.E.A. – PBCP; 1 spec., Malaysia, Benom Mts., 15 kmE of Kampong Dong, 750 m, 3°53'N, 102°01'E, 1.iv.1998, Hauck lgt. – SINGAPORE. BMNH; 1 ♂, Singapore, Parit Satu, at light, 28-29.xi.1960, C.H. Fernando, Brit. Mus. 1961-206.

Extended diagnosis: *Head* (Fig. 1) anterior eyes conspicuously elongated, with distinctly impressed punctured transverse clypeal furrow in form of an acute letter V, with a circular pore on the frons at the bottom of the V; clypeus smooth, with scattered micropunctures, clypeal wing and supraantennal plate smooth, frons with distinct isodiametric reticulation parallel to frontal carinae, reticulation often more indistinct at middle of frons; neck constriction developed as row of punctures, with or without gap at middle; labrum seven-setose; mandible conspicuously elongated, with apex hooked. *Pronotum* with reflexed lateral margin complete, straight but diverging in anterior half; lateral channel of pronotum of same width over entire length, flange convex, three times as wide as basal constriction; disk somewhat dull, distinctly isodiametrically to transversally reticulated, with more or less circular paramedian and paralateral group of punctures restricted to basal half; with posterior angle obtuse but distinct. *Elytron* with intervals one to seven smooth, interval eight with longitudinal reticulation, with distinct tubercle at basal declivity of third interval; striae wide, finely granulated, with punctures indistinct, umbilical setigerous punctures of equal distance, lateral margin at apex about 20% widened. *Male genitalia* (Fig. 14) with aedeagus regularly curved at middle, elongated to apex, at apex with conspicuous and widened securiform lamella, parameres asetose. *Female genitalia* (Fig. 21) with coxostylus regularly curved at apex, with moderately sized cone-like seta preapically, ventro-medially with thirteen nematiform setae, seven of them elongated, laterotergite with four long and one moderately long nematiform setae. *Measurements.* Body length 3.51-4.32 mm ($\bar{x}$ = 3.96 mm*), width 1.21-1.39 mm ($\bar{x}$ = 1.29 mm*), ratio length/width of pronotum 1.0-1.03 ($\bar{x}$ = 1.0*), ratio length/width of elytra 1.61-1.74 ($\bar{x}$ = 1.66*); (*n = 10).

Variability was observed in the extension of the two groups of punctures laterally on the pronotum. Interval eight of the elytron is narrower and flattened at apex in many specimens. The reticulation on interval eight is usually of moderate distinctness but in some specimens it extends more or less to intervals seven and six. The reticulation on the head is restricted to the frons but is in some specimens developed at the frontal furrows, in others it extends more or less to the middle. The V-like sulcus at the middle of the frons is more or less distinctly developed by punctures. The neck constriction is more or less distinctly developed, in some specimens nearly closed and in others with a distinct gap in the middle. The scattered micropunctures on the clypeus are different in number.

Distribution: Hong Kong, South of China, Thailand, Cambodia, Vietnam (South), Malaysia, Singapore.

According to label information, specimens were found from sea level up to an altitude of 750 m. Aston (2016) reports a specimen collected in Hong Kong in moss in a shallow stream.

Type locality: Bangkok.

Remarks: The holotype was found to lack the abdomen. The holotype of *S. paradoxus* collected in Bangkok was not studied. The redescriptive extended diagnosis is based on the comparison of the original description (Putzeys, 1868), the detailed redescription including figuring of the habitus by Andrewes (1929), the two specimens Andrewes compared with the type including the specimen figured by Andrewes, and additional material collected at and near by the type locality. Moreover, 49 additional specimens were available.
In Lorenz (1998, 2005), *Clivina lignicola* Bouchard, 1903 is synonymized with *S. paradoxus*. This synonymization is not followed because the description clearly refers to another species group, most obvious by the large preapical protuberance of the mesotibia. According to current knowledge, *S. paradoxus* was not found in Sumatra as indicated in the description of *Clivina lignicola*. Although the MNHN is given as type depository (Bouchard, 1903), the type could not be located there.

Syleter acutipalpis (Putzeys, 1877)

Figs 8, 15, 22

Psilus acutipalpis Putzeys, 1877: XLVI.
Psilus paradoxus. – Andrewes, 1926: 381. – Andrewes, 1927: 266. – Andrewes, 1929: 387, fig. 58. – Andrewes, 1930: 288.
Syleter paradoxus. – Lorenz, 1998: 138. – Balkenohl, 2001: 30, fig. 39. – Lorenz, 2005: 148 – Balkenohl, 2017: 260.

Type material examined: RBINS; lectotype by present designation: ♂, with labels and data: yellow, handwritten in black ink "Psilus acutipalpis P Birma." / white, handwritten in black ink and printed "Psilus acutipalpis Putz dét. J. Putzeys" / white, violet printed and framed "Soc. Ent. Belg. Coll. Putzeys" / white, handwritten in black ink and printed "Psilus acutipalpis Putz Cotype H. E. Andrewes ~~det.~~ 1928" / red, framed, printed and handwritten in black ink "Paratype de acutipalpis" / white, handwritten in black ink and printed "Psilus paradoxus Putz. = P. acutipalpis Putz. = P. trapezicollis Bates H. E. Andrewes det.".

Additional material: RBINS; 1 ♂, with labels and data: yellow, handwritten in black ink "Birma", white, handwritten in black ink "Cl. Dyschirioides m. Birma", white, violet printed and framed "Soc. Ent. Belg. Coll. Putzeys", white, black printed and handwritten in black ink "Psilus acutipalpis Putz dét. H. E. Andrewes 1920". – NHMB; 1 ♀, handwritten and red framed: China, Lilong.

Extended diagnosis: *Head* anterior eyes moderately elongated, with moderately impressed transverse clypeal furrow and a second furrow in form of a letter V; clypeus, frons, and supraantennal plate smooth; neck constriction complete, developed as distinct sharp step with frons distinctly higher than neck; labrum seven-setose, mandible moderately elongated. *Pronotum* with reflexed lateral margin complete, diverging but slightly convex in anterior half; lateral channel of pronotum from posterior angle to base distinctly widened; basal constriction much wider than carina of flange, flange with acute carina; disk with isodiametric to transverse reticulation, with two groups of punctures laterally with the paramedian one elongated; with posterior angle obtuse but distinct. *Elytron* with all intervals longitudinally reticulated, reticulation with increasing distinctness towards interval eight, with small tubercle at declivity of third interval; striae moderately wide, finely granulated, with punctures indistinct, umbilical setigerous punctures of equal distance, lateral margin at apex about 20% widened. *Male genitalia* (Fig. 15) with aedeagus regularly curved, at apex conspicuously elongated in ventral view, in lateral view developed apically as widely rounded spatula, each paramere bisetose. *Female genitalia* (Fig. 22) with coxostylus regularly curved at apex, with moderately sized cone-like seta preapically, ventromedially with twelve nematiform setae, five of them elongated, laterotergite with three long and two moderately long nematiform setae. *Measurements*. Body length lectotype and additional specimen 3.61 / 3.64 mm, width 1.19 / 1.24 mm, ratio length/width of pronotum 0.99 / 1.01, ratio length/width of elytra 1.65 / 1.61.

Distribution: South of China, Myanmar.

Type locality: Myanmar (Birma).

Remark: The species was described by Putzeys (1877) and synonymized by Andrewes (1929). Putzeys based the description on two specimens. According to Andrewes (1926, 1929), the type was deposited in "the Stettin Museum and a cotype in the Brussels Museum". The cotype is available (RBINS) and has been designated as lectotype for reasons of the stability of the nomenclature. In the lectotype the following body parts are missing: all tarsomeres of the left front leg, left antennomeres with exception of the scapus, right antennomeres from joint six onwards. In addition, the hook at the tip of the mandibles is broken.
The description of Putzeys indicates both specimens came from Calcutta. According to Andrewes (1926) both specimens are labelled "Birma". This is confirmed for the specimen deposited in RBINS.

Syleter fulvaster (Andrewes, 1927)

Figs 9, 16, 23

Psilus fulvaster Andrewes, 1927: 267. – Andrewes, 1930: 288.

Syleter fulvaster. – Lorenz, 1998: 138. – Lorenz, 2005: 148. – Balkenohl, 2001: 29, fig. 38.

Type material examined: *Holotype*: BMNH; ♀, with labels and data: white, printed, black framed "Riam Kanan Martapoera Z.O. Borneo Doherty VI.VII", "Bought from Janson, 1918.", "H.E.Andrewes Coll. B.M. 1945-97.", red, black printed "Type", white, handwritten and printed "Psilus fulvaster Andr. Type H.E.Andrewes det.". Two apical antennomeres are missing on the left side.
Paratype: BMNH; ♂, with same labels and data but with circle, red framed "Cotype".

Additional material: MFNB; 1 ♂, S.O. Borneo Grabowsky. – BMNH; 1 ♂, BORNEO, Sabah near Gum Gum, Lower Kinabatangan, light trap, June 2005, BMNH (E) 2005-178 H. Takano & T. Owen-Edmunds. – NHMW; 1 ♀, Indonesia, SE-Sulawesi, Rawa Aopa Nat. Park Aopa vill., 8.-10.2.1994, leg. M. Strba & I. Jenis. – BMNH; 1 ♀, Tjilatjap Java Drescher 19.IV.1936, And FCD 236, H.E. Andrewes Coll. B.M. 1945-97.

Extended diagnosis: *Head* anterior eyes conspicuously elongated, with moderately impressed transverse clypeal furrow in form of a letter V; clypeus and supraantennal plate nearly smooth, frons with distinct isodiametric reticulation; neck constriction incomplete, developed laterally as row of punctures with a wide gap at middle; labrum three-setose; mandible conspicuously elongated. *Pronotum* with reflexed lateral margin complete, straight but diverging in anterior half; lateral channel of pronotum of same width in its whole length, basal constriction narrow; flange flattened, six times as wide as constriction; disk smooth; with posterior angle completely rounded off but lateral margin knob like thickened. *Elytron* with all intervals smooth, without tubercle at declivity of third interval; striae developed as rows of distinct punctures, distance of umbilical setigerous punctures wider at middle, lateral margin at apex with distinctly widened emargination. *Male genitalia* (Fig. 16) with aedeagus conspicuously curved at middle, at apex flattened and distorted in ventral view, in lateral view spoon-like but asymmetrically widened at apex, rounded at tip of apex, each paramere quadrisetose. *Female genitalia* (Fig. 23) with coxostylus hook-like curved at apex, apically with large cone-like seta, ventromedially with thirteen nematiform setae, four of them elongated, laterotergite with three long and one short nematiform setae. *Measurements*. Body length 2.81-2.84 mm, width 0.93-0.96 mm, ratio length/width of pronotum 1-1.02, ratio length/width of elytra 1.64-1.65; (n = 4).

Distribution: Southeast and central Borneo, Java, Sulawesi.

Type locality: Borneo: Riam Kanan, Martapoera.

***Syleter papua* Darlington, 1962**

Figs 10, 17, 24

Syleter papua Darlington, 1962: 357. – Moore *et al.*, 1987: 78. – Lorenz, 1998: 138. – Lorenz, 2005: 148. – Balkenohl, 2001: 30. – Baehr, 2008: 13, figs 2, 16, 49, 62, 63, 177, 212.

Type material examined: Paratypes: BMNH; 1 ♂, TNHMUK 013460395, white, black printed "Dobodura, Papua, N.G., Mar-July, 1944, Darlington", red, printed "Paratype Syleter papua Darl.", white, printed "Brit. Mus. 1963-26.", circle, yellow framed, black printed "Paratype". – 1 ♀, TNHMUK 013460393, with labels and data white, black printed: "Muffin Bay Dutch N.G. Aug 1944 Darlington", red: "Paratype Syleter papua Darl.", white: "Brit. Mus. 1963-26.", circle, yellow framed, black printed "Paratype". Damaged specimen with right mesotibia, left tarsomeres of the mesotibia, and right antennomeres three to eleven missing. – 1 ♀, BMNH; same data but barcode with No 13460398. Specimen with missing antennomeres three to eleven bilaterally.

Extended diagnosis: *Head* anterior eyes conspicuously elongated, with clypeal furrow slightly indicated by indistinct lateral rugae, smooth at middle, with an indistinct longitudinal pore on frons; clypeus and frons with distinct isodiametric reticulation, supraorbital plate almost smooth; neck constriction almost incomplete, developed as row of punctures with a more or less wide gap at middle; labrum seven-setose; mandible moderately elongated. *Pronotum* with reflexed lateral margin complete, diverging but slightly convex in anterior half; anterior margin excised, anterior angle projecting; lateral channel of pronotum of same width over entire length; basal constriction half as wide as flange, flange convex; disk with reticulation and small group of few punctures; with posterior angle marked as obtuse tooth. *Elytron* with all intervals longitudinally reticulated, with small tubercle at declivity of third interval; striae moderately wide, finely granulated, with punctures indistinct, umbilical setigerous punctures of equal distance, lateral margin at apex about 40% widened. *Male genitalia* (Fig. 17) with aedeagus regularly curved, at apex conspicuously acute in ventral view, in lateral view developed apically as asymmetric distorted spatula curved ventrally, rounded at tip of apex, parameres asetose. *Female genitalia* (Fig. 24) with coxostylus gently curved at apex, with large cone-like seta, ventromedially with eighteen nematiform setae, five of them elongated, laterotergite with three long and two moderately long nematiform setae. *Measurements:* Body length 3.32-3.6 mm; for other measurements see Baehr (2008).

Remark: The species is well described by Darlington (1962) and additional general characters are provided by Baehr (2008) including measurements based on

Figs 7-13. *Syleter* spp., habitus. (7) *S. paradoxus* (Putzeys, 1868), specimen from Bangkok, female. (8) *S. acutipalpis* (Putzeys, 1877), lectotype. (9) *S. fulvaster* (Andrewes, 1927), paratype, male. (10) *S. papua* Darlington, 1962, paratype, female. (11) *S. sinepunctatus sinepunctatus* sp. nov., holotype. (12) *S. sinepunctatus kluangensis* ssp. nov., holotype. (13) *S. gradus* sp. nov. holotype.

ten specimens, and description of the male and female genitalia. The ink sketches of the male genitalia and the shape of the female coxostyli in general reflect more or less the reality. However, the two females investigated show a different setae pattern as figured in Baehr (2008), and the subapical setose organ figured could not be observed (500 fold, Polyvar compound microscope with optimized condenser). The female specimens investigated by Baehr (2008) were from Dobodura whereas the females investigated in this contribution were found in the Indonesian part of the island (Vogelkop). Therefore it is possible the two populations belong to different forms.

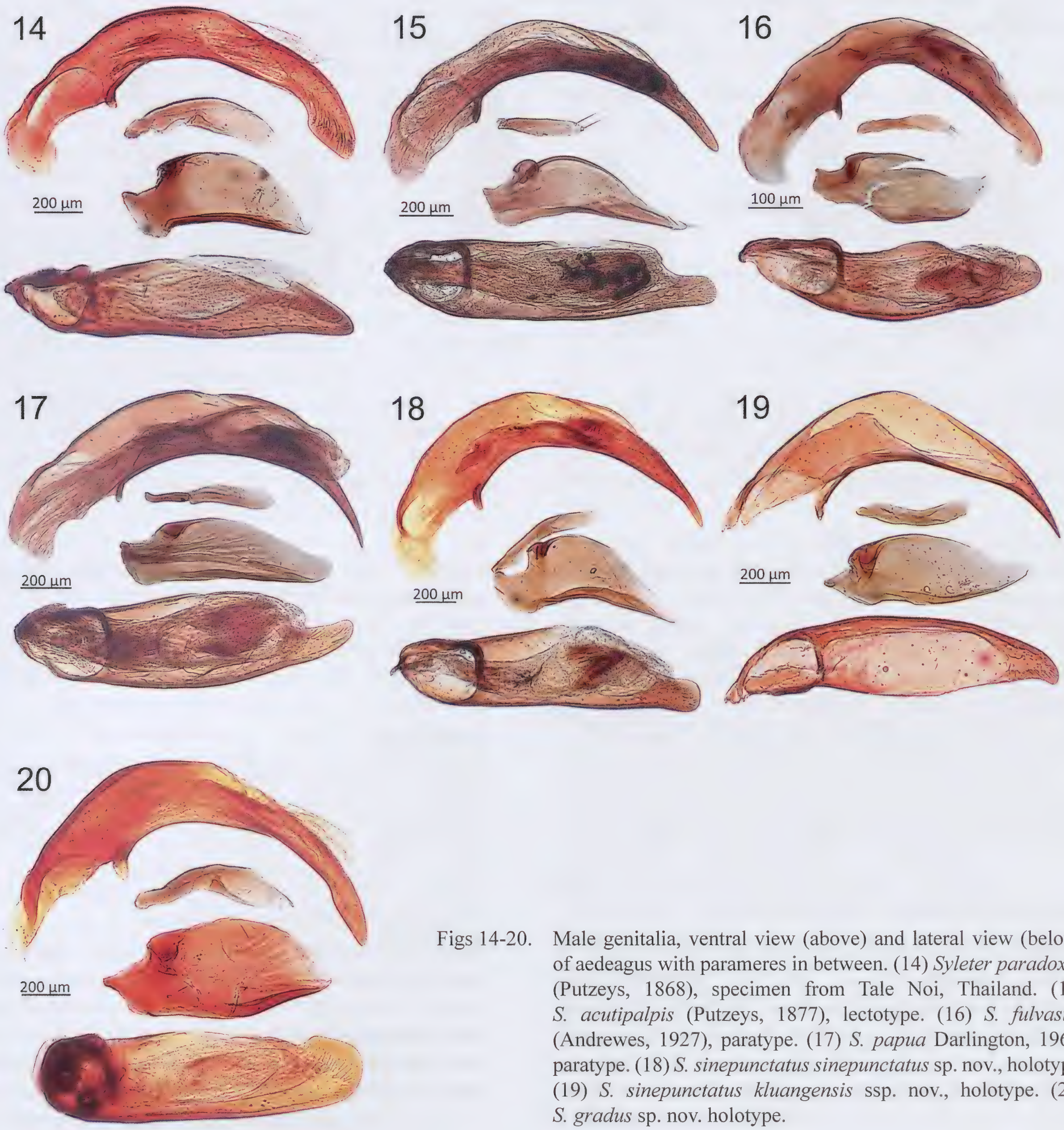
Distribution: New Guinea: Papua-New Guinea: Dobodura; Indonesia: Muffin Bay (Darlington, 1962). Northeast Australia (Queensland): Cape York (Moore, 1987; Baehr, 2008).

Type locality: Dobodura in Papua-New Guinea.

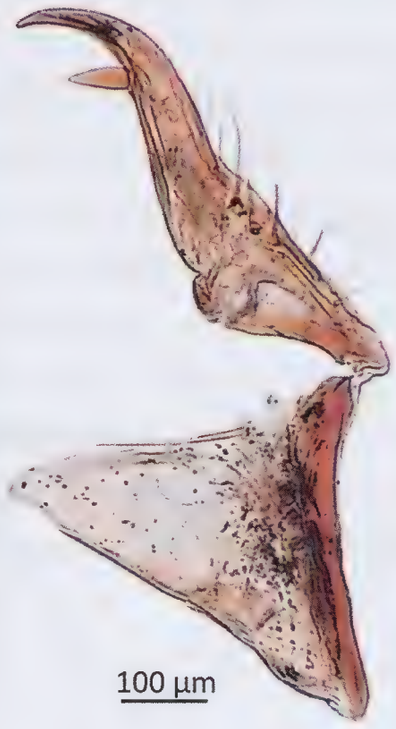
Syleter sinepunctatus sinepunctatus sp. nov.

Figs 11, 18, 25

Holotype: BMNH; ♂, with labels and data: white, handwritten in black ink "32 BRUNEI Bukit Sulang Nn hamunin, 28.VIII.-5.IX.82, B.E. Stork B.M. 1982-388", printed "at light".



Figs 14-20. Male genitalia, ventral view (above) and lateral view (below) of aedeagus with parameres in between. (14) *Syleter paradoxus* (Putzeys, 1868), specimen from Tale Noi, Thailand. (15) *S. acutipalpis* (Putzeys, 1877), lectotype. (16) *S. fulvaster* (Andrewes, 1927), paratype. (17) *S. papua* Darlington, 1962, paratype. (18) *S. sinepunctatus sinepunctatus* sp. nov., holotype. (19) *S. sinepunctatus kluangensis* ssp. nov., holotype. (20) *S. gradus* sp. nov. holotype.



Figs 21-27. Female coxostyli with laterotergite. (21) *Syleter paradoxus* (Putzeys, 1868), specimen from Tale Noi, Thailand, with latero- and mediotergite. (22) *S. acutipalpis* (Putzeys, 1877), specimen from Lilong, China. (23) *S. fulvaster* (Andrewes, 1927), holotype. (24) *S. papua* Darlington, 1962, paratype. (25) *S. sinepunctatus sinepunctatus* sp. nov., paratype. (26) *S. sinepunctatus kluangensis* sp. nov., paratype. (27) *S. gradus* sp. nov. paratype.

Paratypes: BMNH; 1 ♀, with labels and data: orange, handwritten in black ink "Kuching SARAWAK 28.7.1961", "at light", white, black printed "R.O.S.Clarke. B.M. 1970-557.", green, handwritten with pencil "Syleter n.sp. nr. paradoxus PUTZ. det. Balkenohl, 2000". – MFNB; 1 ♀, with labels and data: beige, black printed "S.O. Borneo Grabowsky.", "Zool. Mus. Berlin". – ADCW; 3 ♂♂, 2 ♀♀, 7 specimens., with labels and data: white, black printed "INDONESIEN: Kalimantan Timur, Tanjung Isuy 20.1.1995 leg. Seyfert & Greindl (34)". – ADCW; 1 ♂, 3 ♀♀, 5 specimens, same data but "(33)" and "(34)" and orange, handwritten: "Coll. Zettel Wien".

Diagnosis: A medium sized species with seven-setose labrum, and the clypeus and frons isodiametrically reticulated. Differentiated from the similar species *S. paradoxus* and *S. gradus* sp. nov. by the missing punctures on the disk of the pronotum and the missing clypeo-frontal furrow. *S. paradoxus* differs in addition by the smooth clypeus. *S. gradus* sp. nov. differs in addition by the complete and step-like developed neck constriction, and by the larger size.

Etymology: The name refers to the completely missing punctures on the disc of the pronotum (Latin: sine – without).

Description

Measurements: Body length 3.37-3.8 mm ($\bar{x}$ = 3.64 mm*), width 1.16-1.27 mm ($\bar{x}$ = 1.22 mm*), ratio length/width of pronotum 1.01-1.05 ($\bar{x}$ = 1.03*), ratio length/width of elytra 1.58-1.66 ($\bar{x}$ = 1.62*); (*n = 10).

Colour: Piceous to fuscous. Legs fuscous. Antenna, tarsomeres and palpomeres testaceous.

Head: A third narrower than pronotum, frons and clypeus anterior eye-level conspicuously elongated. Clypeus straight anteriorly, with lateral angle obtuse rounded; completely fused with clypeal wing and supraantennal plate, all reflexed margined, clypeus convex, separated from elongated convex supraantennal plate by parallel running deep and conspicuously wide clypeal furrows,

extending up to anterior eye-level; supraantennal plate extended up to mid-eye level; clypeus separated from frons by indistinct transverse nearly not traceable change of the direction of the convexity. Frons moderately convex, with wide frontal furrows, with distinct lateral carina separating frontal furrow from supraorbital furrow, frontal furrow and lateral carina wide, slightly diverging and extending nearly up to neck constriction. Clypeal, frontal, and supraorbital furrow not connected. Clypeus and frons with distinct isodiametric reticulation, clypeal wing and supraantennal plate with longitudinal reticulation. Neck at middle at same level as frons, constriction developed laterally as row of punctures. Eye moderately projecting laterally. Gena indistinct. Antenna reaching over posterior angle of pronotum, antennomeres four to ten elongate (around 1.8 times longer than wide). Labrum straight anteriorly, reticulated, seven setose.

Pronotum: Disk in lateral view moderately convex, convex in frontal view. Outline trapezoid. Reflexed lateral margin smooth, nearly straight attenuated in anterior half, widest at posterior third; anterior angle slightly projecting; posterior angle developed as distinct rounded tooth, tooth laterally much less projecting than widest part of lateral margin. Lateral channel as wide as reflexed lateral margin, anterior setigerous punctures removed from channel by diameter of pore, posterior setigerous puncture situated in the channel close to the tooth of the posterior angle. Median line moderately narrow; anterior transverse line slightly wider than median line, joining with median line. Surface with isodiametric to transverse reticulation; basal constriction distinct, flange 2.5 times wider than constriction.

Elytron: Disk slightly convex in anterior half in lateral view, convex on frontal view. Around 1.6 times as long as wide, slightly dilated in apical half, maximum width slightly behind middle. Reflexed lateral margin smooth. Scutellar striole short but visible. Base of elytron with setigerous tubercle at base of second interval, with a small tubercle at base of third interval. Striae moderately deep, crenulate-striate, four to seven reaching base, the seventh at level of the humerus, humerus marked by distinct tooth. Stria one running to apex, six and seven joining apically, the others partly joining at apex (variable). Intervals moderately convex. Third interval with three setigerous punctures, first distinctly removed from base and approaching third stria, the second situated at middle of the interval, the third approaching second stria. Interval one to seven smooth, glossy, interval eight with indistinct longitudinal reticulation.

Hind wings: Fully developed.

Lower surface: Proepisternum covered with isodiametric reticulation and few transverse wrinkles. Sternites of abdomen transversely sulcate, with transverse reticulation.

Legs: Profemur dorsally sulcate. Protibia covered with longitudinal reticulation, with two slender spines of moderate length, the third one obtuse, movable spur regularly arcuate.

Male genitalia (Fig. 18): Median lobe regularly curved in basal half, gently curved towards apex, apically distinctly acute in ventral view, in lateral view widened at middle, developed apically as asymmetric distorted spatula, broadly rounded at tip of apex; endophallus with two longitudinal groups of bristles; parameres asetose.

Female genitalia (Fig. 25): Coxostylus one and two partly fused; coxostylus two gently curved at apex, ventromedially conspicuously narrowed and with conspicuously wide and long nematiform seta, apically with moderately large cone-like seta, with twelve long and one short nematiform setae, coxostylus one with two long nematiform apical setae, ventromedially with four moderately long setae, with two shorter setae at middle; laterotergite with five moderately long nematiform setae, one of them situated basally.

Variability: The reticulation on interval eight is more or less distinct. At the apex of the elytron the striae two to five are more or less joining.

Distribution: Known from two locations in Borneo (Brunei and South East Borneo).

***Syleter sinepunctatus kluangensis* ssp. nov.**

Figs 12, 19, 26

Holotype: BMNH; ♂, with labels and data: white, printed and handwritten in black ink "WEST MALAYSIA Jahore Kluang" and backside "m. V. Trap", "MARDI M9918 27-483 TAX. EXPDN." and backside "Piper nigrum", "Pres by Comm Inst Ent B.M. 1983-1", yellow, black printed "C.I.E. COLL. A. 15326", white, black printed and handwritten "Syleter sp. det. R.B. Magde, 1983", green, handwritten in pencil "Syleter n.sp. Balkenohl 2000".

Paratype: NHMG; 1 ♀, with labels and data: white, printed "Selangor Sungei Buloh Kuala Lumpur 20-IX-72 T. Jaccoud".

Diagnosis: The subspecies differs from the nominotypical subspecies mainly by the elytron with its slightly more convex lateral margin, the indistinct reticulation on the lateral intervals, the wider frontal furrows of the head, and the pronotum with its smaller posterior angle. In addition, the apex of the aedeagus is acutely pointed at the tip and turns dorsally. In contrast to the nominotypical subspecies it is not found in Borneo.

Etymology: The name is a noun and refers to the type locality, Kluang in West Malaysia.

Description:

Measurements: Body length 3.45 / 3.59 mm, width 1.15 / 1.26 mm, ratio length/width of pronotum 1.0 / 0.99, ratio length/width of elytra 1.59 / 1.55.

The subspecies differs from the nominotypical subspecies in the following characters:

Head: Frontal furrow widened towards the middle at the front.
Pronotum: Posterior angle indistinct, obtuse.
Elytron: Lateral margin indistinctly subcrenulated, convex at middle, maximum width at middle; intervals with indistinct reticulation on intervals five to seven with increasing distinctness towards interval eight.
Male genitalia (Fig. 19): Median lobe apically conspicuously acute in ventral view, in lateral view acuminated and asymmetric curved dorsally.
Female genitalia (Fig. 26): Laterotergite with four long and one small nematiform setae.

Distribution: Known from West Malaysia (Kluang in Jahore, and Sungei Buloh near Kuala Lumpur).

Syleter gradus sp. nov.

Figs 13, 20, 27

Holotype: BMNH; ♂, white, handwritten in black ink "Talang Borneo Grabowsky I. 82", black printed "H.E.Andrewes Coll. B.M. 1945-97.", white, black handwritten and printed "Psilus acutipalpis Putz. Compared with type H.E.A.", black printed "H.E.Andrewes Coll. B.M. 1945-97.".

Paratypes: BMNH; 1 ♀, white, handwritten in black ink "Talang Borneo Grabowsky", black printed "H.E. Andrewes Coll. B.M. 1945-97.". – ADCW; 5 ♀♀, with labels and data: white, black printed "INDONESIEN: Kalimantan Timur, Tanjung Isuy 20.1.1995 leg. Seyfert & Greindl (33)", orange, handwritten "Coll. Zettel Wien".

Diagnosis: A larger sized species with seven-setose labrum, and the clypeus and frons isodiametrically reticulated. Differentiated from the similar species *S. paradoxus* and *S. sinepunctatus sinepunctatus* sp. nov. by the stepped and complete neck constriction, the longitudinal reticulation of the intervals one to seven, and the larger size. In addition, in *S. sinepunctatus sinepunctatus* sp. nov. the punctures on the disk of the pronotum are missing, and in *S. paradoxus* the clypeus is not reticulated.

Etymology: The name is a noun and refers to the stepped neck constriction (Latin: gradus – step).

Description

Measurements: Body length 4.25-4.66 mm ($\bar{x}$ = 4.41 mm*), width 1.32-1.55 mm ($\bar{x}$ = 1.46 mm*), ratio length/width of pronotum 0.99-1.02 ($\bar{x}$ = 1.01*), ratio length/width of elytra 1.62-1.72 ($\bar{x}$ = 1.67*); (*n = 7).
Colour: Piceous to fuscous. Intermediate and hind leg fuscous. Antenna, tarsomeres and palpomeres testaceous.
Head: A third narrower than pronotum, frons and clypeus anterior eye-level conspicuously elongated. Clypeus straight anteriorly, with lateral angle obtuse rounded; completely fused with clypeal wing and supraantennal plate, all reflexed margined, clypeus flattened, separated from elongated convex supraantennal plate by parallel running deep and wide clypeal furrows, slightly diverging posteriorly, extending up to a quarter of anterior eye-level; supraantennal plate extended up to mid-eye level, clypeus separated from frons by a distinct transverse line of partly fused punctures and obtuse flat furrow, furrow turning posteriorly in form of an acute letter V, with a longitudinal pore on the frons at the bottom of the V. Frons moderately convex, with wide frontal furrow, with distinct lateral carina separating frontal furrow from supraorbital furrow, frontal furrow and lateral carina wide, distinctly diverging and extending up to neck constriction. Clypeal, frontal, and supraorbital furrows not connected. Clypeus, clypeal wing, and frons with distinct isodiametric reticulation, supraantennal plate smooth, with small depression posteriorly. Neck at middle deeper than frons, constriction developed as distinct step. Eye laterally distinctly projecting. Gena indistinct. Antenna reaching up to base of pronotum, antennomeres four to ten elongate (around twice as long as wide). Labrum distinctly convex anteriorly, reticulated, seven setose.
Pronotum: Disk in lateral view moderately convex, convex in frontal view but slightly flattened at median line. Outline oblongo-trapezoid. Reflexed lateral margin smooth, straight to slightly convex attenuated in anterior half, widest at posterior third; anterior angle not projecting; posterior angle developed as distinct obtuse tooth, tooth laterally much less projecting than widest part of lateral margin. Lateral channel as wide as reflexed lateral margin, anterior setigerous puncture located directly beside the channel, posterior setigerous puncture situated in the channel close to the tooth of the posterior angle. Median line moderately narrow; anterior transverse line slightly wider than median line, joining with median line. Surface with isodiametric to slightly transverse reticulation, with longitudinal paramedian and paralateral band of punctures; basal constriction distinct, flange more than three times wider than constriction.
Elytron: Disk flattened in anterior half in lateral view, convex on frontal view. Around 1.7 times as long as wide, lateral margin nearly parallel at middle, maximum width at middle. Reflexed lateral margin crenulated. Scutellar striole short, indistinct. Base of elytron with setigerous tubercle at base of first stria, with a small tubercle at base of third interval. Striae moderately deep, crenulate-striate, four to seven reaching base, the seventh at level of the humerus, humerus marked by distinct tooth. Stria one running to apex, two ending free at apex, three and four joining, five, six, and seven ending free apically. Intervals moderately convex, eighths slightly carinate apically. Third interval with three setigerous punctures, first distinctly removed from base and approaching third stria, the second and third approaching second stria. All intervals longitudinally reticulated, reticulation more intensive laterally.
Hind wings: Fully developed.

Lower surface: Proepisternum covered with isodiametric reticulation and few transverse wrinkles. Sternites of abdomen slightly transversely sulcate, with transverse reticulation.
Legs: Profemur dorsally sulcate. Protibia sulcate, covered with longitudinal reticulation, with three slender spines of moderate length, movable spur regularly arcuate.
Male genitalia (Fig. 20): Median lobe in ventral view distinctly and regularly curved in basal half, elongated in apical third, apex conspicuously securiform, in lateral view slightly widened at middle, apex developed as asymmetric slightly distorted wide hatchet, broadly rounded at tip of apex; endophallus with a longitudinal group and three small groups of bristles; parameres asetose.
Female genitalia (Fig. 27): Coxostylus one and two partly fused; coxostylus two gently curved at apex, ventromedially distinctly narrowed and with conspicuously wide and moderately long nematiform seta, apically with small cone-like seta, with thirteen long and one short nematiform setae; coxostylus one with two long nematiform apical setae, ventromedially with five moderately long setae, with six shorter setae at middle; laterotergite with three long, and two short setae, and with one long seta situated basally.
Variability: On the head, the V-shaped transverse line between the clypeus and frons shows more or less fewer punctures and is more or less impressed. On the pronotum the paramedian and paralateral band punctures varies regarding the number of punctures and the bands can be more or less wide and more or less extended nearly up to the anterior margin. The crenulation at the lateral margin of the elytron shows variability in their distinctness.

Distribution: Known from two locations in the Indonesian part of Borneo.

Specimens incertae sedis: MNHN; 2 specimens, labels with identical handwriting in black ink: Sumatra Palembang. One with additional label "Syleter sumatraensis".
Remark: Both specimens are incomplete and in bad condition with broken elytra and missing abdomen. One is obviously a female due to some remains in the hind body. *S. sumatraensis* is not a valid name. – MFNB; 1 ♀, with labels and data: S.O. Borneo Grabowsky, Zool. Mus. Berlin. This incomplete specimen is close to *S. sinepunctatus* but might represent a new species.

Genus *Parasyleter* gen. nov.

Figs 2, 5, 28, 29, 30

Type species: *Dyschirius doriae* Putzeys, 1873: 14.

Genus diagnosis: *Size* 1.8 to 2.3 mm. *Head* (Fig. 2) with clypeus and frons distinctly elongated and flattened anteriorly; clypeus and clypeal wing fused, delimitation between clypeal wing and supraantennal plate observable as indistinct obtuse notch in two of the species; clypeus straight or slightly convex anteriorly, as far as or slightly more projecting than clypeal wing; mandible elongated, narrow in apical third, laterally nearly straight or convex, hooked at apical tip; labrum three- or five-setose; maxillary palpomere distinctly narrowed and slender towards apex, nearly straight, two apical segments securiform; antenna with scapus and pedicellus eccentrically attached; eye without or with distinct reduction, gena small or extended posteriorly. Mentum not elongated, with lateral lobe convex, median tooth as wide as lateral lobe, acute, distinctly more projecting than lateral lobe, surface with slight transverse rugae. *Pronotum* square or indistinctly trapezoid, with reflexed lateral margin incomplete, running from anterior angle up to posterior setigerous puncture, posterior angle rounded off without tooth, lateral channel of equal width, median line narrow, finely or just not joining basal constriction; proepisternum visible basally in dorsal view; flange at base convex, as narrow as or up to two times as wide as basal constriction. *Elytron* with interval eight convex, lateral channel distinctly flared apically, with interval eight distinctly emarginated apically and row of umbilical setigerous punctures distinctly following the emargination, interval eight with distinct emarginated carina at apex; third interval without setigerous punctures. *Hind wings* fully developed or reduced. *Legs* with front and intermediate tarsomeres slightly widened, more distinct in males; mesotibia with four setae laterally, preapical seta either without any protuberance or arising from minute tubercle (Fig. 5). *Male genitalia* (Fig. 29) with aedeagus distinctly curved, apical part elongated, apex more or less spatulate or securiform. *Female genitalia* (Fig. 30) with coxostylus one and two completely fused, with evident cone-like seta in apical third; laterotergite with isolated setae.

Differential diagnosis: See key to the genera.

Etymology: The name is a combination of the Greek adjective para- (besides) and the original genus name.

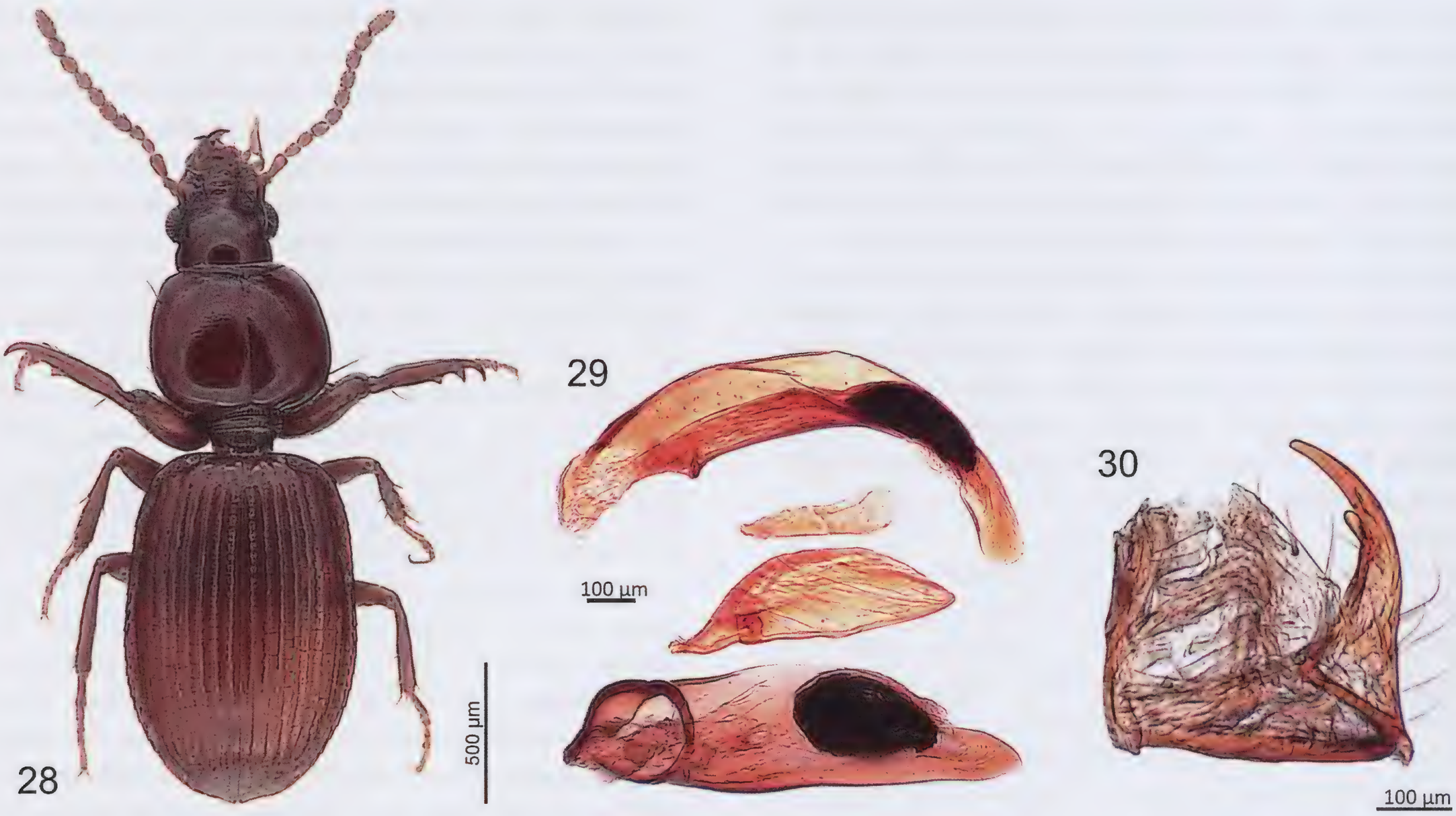
Species: Three described species belong into the genus: *Dyschirius doriae* Putzeys, 1873 known from Indonesia (Figs 2, 5, 28, 29, 30), *Psilus malayicus* Andrewes, 1927 distributed in Malaysia, and *Psilus porphyreus* Andrewes, 1923 known from Sri Lanka. The genus includes also species not described yet and is currently in revision by the author.

Genus *Clypeuspinus* gen. nov.

Figs 3, 6, 31, 32

Type species: *Psilus validus* Andrewes, 1936: 202.

Genus diagnosis: *Size* 4.8 mm. *Head* with clypeus and frons conspicuously elongated, convex; clypeus, clypeal wing, and supraantennal plate separated by obtuse



Figs 28-30. *Parasyleter doriae* (Putzeys, 1873) comb. nov., specimen from Sarawak collected by G. Doria. (28) Habitus, male. (29) Male genitalia, ventral view (above) and lateral view (below) of aedeagus with parameres in between. (30) Female coxostyli and laterotergite.

notch; clypeus straight and sloping anteriorly, clypeal wing conspicuously projecting anteriorly; mandible distinctly elongated, narrow in apical third, laterally convex, regularly convex in apical half, bent dorsally; labrum five-setose; maxillary palpomere elongated, slightly securiform; antenna with scapus and pedicellus eccentrically attached; eye relatively flat but not reduced, not projecting laterally, gena as long as eye. Mentum moderately elongated, with lateral lobe wide and convex, median tooth obtuse angled, projecting as far as lateral lobe, surface with rough longitudinal rugae. *Pronotum* with pentagonal longitudinal outline, with reflexed lateral margin complete, running from anterior angle up to basal constriction, posterior angle with moderately acute tooth projecting laterally, lateral channel distinctly widened between the two lateral setigerous punctures, median line wide, joining broadly basal constriction, proepisternum invisible in dorsal view, flange at base carinate, as wide as basal constriction. *Elytron* with interval eight carinate from humerus to apex; lateral channel of equal width from humerus to apex; third interval with three (left side) respectively four (right side) setigerous punctures. *Hind wings* fully developed. *Legs* with tarsomeres not widened (one female investigated); mesotibia with long protuberance preapically furnished with seta. *Male genitalia* unknown. *Female genitalia* with coxostylus one and two nearly completely fused, without cone-like seta.

Differential diagnosis: See key to the genera. However, the most similar species are *Basilewskyana villiersi* Basilewsky, 1948 and *B. brittoni* Kult, 1959 both from West Africa. These two species are completely black and much larger (7.2 and 7.8 mm). In addition, they differ mainly by a cylindrical shape, the clypeal wings slightly projecting, a deep facial furrow with distinct facial carina, without any clypeal suture, a wider labrum, the elytron with missing humeral tooth, more convex intervals, and the elytral setigerous punctures situated in the middle of the third interval. Members of the American genus *Ardistomis* Putzeys, 1846 also show a considerable elongation of the anterior part of the head and their mandibles are evidently elongated. But the maxillary palpomeres and the widened tarsomeres of the front and intermediate legs are very similar to *Syleter*. However, the pronotum, elytron and the plica at the apex of the elytron is very different.

Etymology: The name is a combination of two nouns, clypeus and spinus. Clypeus points to the conspicuously lobate-like projecting clypeal wings. Spinus highlights the long protuberance at the mesotibia (Latin: spinus – spur).

Clypeuspinus validus (Andrewes, 1936) comb. nov.

Figs 3, 6, 31, 32

Psilus validus Andrewes, 1936: 202.

Syleter validus. – Lorenz, 1998: 138. – 2005: 148. – Balkenohl, 2001: 30. – Balkenohl, 2021a: in press.

Type material examined

Holotype: BMNH; ♀, with labels and data: white, handwritten in black ink "Battaramulla W.P. Ceylon 7-V-30", white, handwritten in black ink "3520", white, black printed "Brit. Mus. 1936-628", white, circle, red framed and black printed "Type", white, handwritten in black ink "Psilus validus Andr. Type H. E. Andrewes det.", white, handwritten in blue ink "Oxygnathus validus Andr. det. K. Kult 47". The two apical tarsomeres of the left mesotibia and the right hind tibia with tarsomeres are missing. The holotype is the only available material.

Redescription

Measurements: Body length 4.81 mm; width 1.46 mm; ratio length/width of pronotum 0.98; ratio length/width of elytra 1.75.

Colour: Dorsal and ventral surface glossy; piceous with fuscous tinge; clypeus, wing of clypeus, supraantennal plate, and mandible fuscous, other mouthparts, antenna and legs paler yellowish-fuscous.

Head (Fig. 3) with dorsal surface smooth, with scattered micropunctures. One third narrower than pronotum, conspicuously elongated. Clypeus with middle part narrower than labrum, with straight and anteriorly sloping margin, with indistinct clypeal suture, wing of clypeus moderately wide, conspicuously lobate-like projecting anteriorly, separated from clypeus by obtuse emargination, clypeal setigerous punctures situated in deep frontal furrows (setae rubbed off but the setigerous punctures are visible). Supraantennal plate vaulted, elongated, anteriorly separated from clypeal wing by indistinct notch, reflexed margined in posterior half. Frons elongated anteriorly, moderately convex. Supraorbital furrow deep, wide, converging at middle of eyes, bilaterally with two supraorbital setae situated at posterior eye- and posterior gena-level. Supraorbital carina blunt. Frontal furrow wide, well impressed. Neck constriction nearly complete, composed of bigger punctures. Eye of regular size, somewhat flattened in dorsal view but moderately convex in lateral view. Gena broad, conspicuously elongated, surface with few irregular rugae. Antenna not elongated, reaching to middle of pronotum, antennomere two slightly longer than three, attached eccentrically to scapus, scapus with indistinct irregular reticulation, with the seta situated

Figs 31-32. *Clypeuspinus validus* (Andrewes, 1936) comb. nov., holotype. (31) Habitus. (32) Female coxostyli with laterotergite.

dorso-frontally at apical quarter. Labrum slightly pointed anteriorly, five-setose, with indistinct irregular reticulation. Mandible conspicuously elongated, falcate, bend slightly dorsally, scrobe visible in dorsal view. Apical segment of maxillary palpus slender, moderately elongated, slightly securiform. Segment two of labial palpus bisetose. Ligula pointed, deeply embedded. Mentum with lobes carinate, moderately wide, convex anteriorly, epilobe narrow, with pointed central tooth projecting as far as lateral lobe, surface with rough rugae.

Pronotum: Outline longitudinal pentagon-like, flattened on disc (lateral view), moderately convex in frontal view. Anterior angle projecting. Posterior angle marked by a distinct tooth which interrupts the lateral channel and projects laterally. Reflexed lateral margin straight in anterior half, diverging posteriorly, gently convex posteriorly to posterior angle, reaching from anterior angles up to base. Marginal channel distinctly widened between the two lateral setigerous punctures, foveolate. Lateral anterior setigerous puncture situated in distinct fovea in the channel, posterior one slightly removed from channel. Reflexed margin narrow, with indistinct notches. Proepisternum just visible posteriorly in dorsal view. Anterior transverse line deep, composed of punctures, joining with median line. Median line deep, moderately wide, distinctly joining base. Surface with distinct transverse wrinkles, with scattered micropunctures, with isodiametric reticulation in basal third, at base vaulted laterally. Flange narrow, carinate, as wide as basal constriction.

Elytron: Outline subelongate, flattened on disk in anterior half (lateral view). Lateral margin nearly straight in anterior half, slightly contracted to base and regularly convex in apical half, maximum width slightly behind middle. Humerus distinct, with distinct humeral tooth. Base convex. Reflexed lateral margin smooth, marginal channel with uninterrupted series of setigerous punctures. Stria one with setigerous tubercle at base of first stria, with distinct tubercle at base of third interval. Scutellar stria moderately developed. Striae moderately deep, punctato-striate; stria one joining basal tubercle, stria two and three free at base. Striae one and seven reaching apex, two to six ending apically at vault of interval seven. Intervals convex, convexity more evident laterally, eighth carinate from humerus nearly up to apex, seventh carinate at humerus. Third interval with three setigerous punctures on the left and with four punctures at the right elytron, all approaching more or less third stria, setae upright, of moderate length. Surface of intervals with indistinct isodiametric reticulation, slightly more distinct at outer intervals.

Hind wings: Fully developed.

Ventral surface: Proepisternum indistinctly isodiametrically reticulated, with transverse rugae. Last four tergites with two accessory setae at middle, with transverse reticulation, terminal segment with the two apical setigerous punctures widely separated.

Legs: Protibia with the three terminal spines long, slender, curved distinctly laterally; movable spur nearly as long as spine, turned slightly ventrally, surface with slight sulcus and isodiametric to longitudinal reticulation. First tarsomere of front leg longer than tarsomeres two to four together. Intermediate tibia with long protuberance preapically furnished with seta (Fig. 6). Tarsomeres of front and intermediate leg not widened.

Male genitalia: Unknown.

Female genitalia: With coxostylus one and two nearly completely fused (Fig. 32), moderately broadened at base, slightly curved in apical half, dorsally with nine long and slender and one distinctly elongated and robust nematiform setae in the middle part, ventrally with six smaller setae, no subapical setose organ. Laterotergite with four long nematiform setae.

Variability: The number of setigerous punctures on interval three of the elytra is different (three and four setae).

Distribution: Known from the type locality in Battaramulla, Western Province of Sri Lanka.

DISCUSSION

The characterization of *Clypeuspinus* gen. nov. raises the question of its relationship. The existence of the long protuberance at the mesotibia, the shape of the mandible and maxillary palpus, the different type of the mentum, the anteriorly projecting clypeal wings with the clypeus in between sloping, the wide foveolate lateral channel of the pronotum, the regular lateral channel of the elytron at apex, and the different coxostyli clearly demonstrate the genus differs extraordinarily from *Syleter* or *Parasyleter* gen. nov.

However, it is clearly a genus among the subtribe Clivinini (according to Kryzhanovskij, 1976, 1983, Baehr, 2008). So, the question of the taxonomical position of *Clypeuspinus* gen. nov. among the Clivinini is challenging. In contrast to the Scaritinae, phylogenetic assessments are available only for some Clivinini groups [e.g., *Schizogenius* Putzeys, 1846 (Whitehead, 1972), *Trilophus* Andrewes, 1927 (Balkenohl, 1999)] but no comprehensive phylogenetic assessment for the subtribe is available at present. Therefore, relationships are described historically and until today on the basis of similarities observed when genera and species are compared, morphologically. This approach has been shown to be correct over wider groups but it also reflects opinions because a general stringent assessment is missing. For the comparison of *Clypeuspinus* gen. nov. and in the absence of a better tool the traditional approach has been followed.

When looking at the Oriental Clivinini, the eye-catching anteriorly projecting clypeal wings with the sloping clypeus in between is found also in *Sparostes* Putzeys, 1867 but without matching of all the other characters.

This similarity was also seen by Andrewes (1936) when he described the species *validus*.

Comparing Oriental genera more closely, an anteriorly somewhat elongated head with deep frontal furrows, the flattened eyes with the genae distinctly elongated, falcate mandibles, the type of the maxillary palpus, and a spur at the mesotibia can be found in *Oxygnathus* Dejean, 1826. This is obviously the reason why Kult added a handwritten label under the holotype specimen with the following content: "Oxygnathus validus Andr. det. K. Kult 47" by underlining *Oxygnathus*. However, in *Oxygnathus* the head is anteriorly only slightly prolonged, the clypeal wings are slightly projecting over the level of the clypeus, and in the antennae the scapus and pedicellus are not eccentrically attached. The asetose scapus shows a specialized shape with a short basal part and nearly right angled flexed very long apical part. This is also true for *Oxygnathopsis* Louwerens, 1953 but to a somewhat different degree.

So, there is no genus in the Oriental region to which *Clypeuspinus* gen. nov. is more closely similar. This astonishing finding resulted in a comparison against the African, Australian, and Neotropical genera. Among the genera of these three regions there is one genus most similar to *Clypeuspinus* gen. nov. It is *Basilewskyana* Kult, 1959 known with the two described species *B. villiersi* Basilewsky and *B. brittoni* Kult, both from West Africa, sharing many of the basic characters including the type of fused coxostyli. The male genitalia could not be compared because the female holotype of *C. validus* is unique and no other material is available.

The two Oriental genera, *Syleter* Andrewes and *Parasyleter* gen. nov. are separated mainly by the pronotum, the different type of the female coxostyli, and the mentum with the characters given in the key provided above. Exactly these different characters of the pronotum served Jeannel (1957) for recognizing different phyletic lines and genera (i.e. among Reicheiina). It basically also separates the genera *Trilophus* Andrewes from *Trilophidius* Jeannel, 1957.

In both of the African groups, *Syleter* Andrewes and *Afrosyleter* Basilewsky, 1959, the reflexed lateral margin of the pronotum runs from the anterior angles up to the basal constriction, the median line is complete at the base, and the proepisterna are not visible in dorsal view. The two genera were separated by Basilewsky (1959) mainly due to a smaller and subparallel pronotum with more or less toothed posterior angles, the serrulate elytra, and the presence of four setigerous punctures on interval three. In addition, the male aedeagus demonstrated a completely different type in *Afrosyleter* with both of the parameres bisetose.

Relationships of *Syleter* with the genus *Ancus* Putzeys, 1867 are supposed by Baehr (2008) because of the "similar securiform palpi". However, the palpi in *Ancus* are distinctly shorter and not as pointed apically as in *Syleter* and *Parasyleter*. Moreover, all the other features characterizing *Syleter* and *Parasyleter* do not match with *Ancus*.

It is believed *Syleter* and *Parasyleter* belong to a circle of small Oriental clivinid genera including *Trilophus* Andrewes, *Trilophidius* Jeannel, and *Leleuporella* Basilewsky, 1956.

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REFERENCES

Andrewes H.E. 1923. Descriptions of some new Carabidae from Ceylon. *Spolia Zeylanica* 12: 223-251.

Andrewes H.E. 1926. Papers on Oriental Carabidae. – XVII. *The Annals and Magazine of Natural History* 9: 371-381.

Andrewes H.E. 1927. Papers on Oriental Carabidae. – XX. *The Annals and Magazine of Natural History, including Zoology, Botany, and Geology,* Ninth Series 20: 263-272.

Andrewes H.E. 1929. The fauna of British India, including Ceylon and Burma. Coleoptera, Carabidae, Vol. I., Carabinae. *Taylor & Francis, London*, 431 pp.

Andrewes H.E. 1930. Catalogue of Indian Insects. Part 18 - Carabidae. *Government of India Central Publication Branch Calcutta*, 389 pp.

Andrewes H.E. 1936. Descriptions of some new Carabidae from Ceylon (Part III). *Spolia Zeylanica* 19: 201-209.

Andrewes H.E. 1941. Papers on Oriental Carabidae. – XXXVII. *The Annals and Magazine of Natural History* 11: 307-317.

Aston P. 2016. Catalogue and Bibliography of the Honk Kong Carabidae Latreille, 1802 (Coleoptera: Adephaga), with notes on the historic boundaries of Hong Kong as related to zoological collections. *Zootaxa* 4121: 201-257.

Baehr M. 2008. The Australian Clivinini 1. The genera *Ancus* Putzeys, *Aspidoglossa* Putzeys, *Clivinarchus* Sloane, *Platysphyrus* Sloane, *Pseudoclivina* Kult, *Rhysocara* Sloane, *Syleter* Andrewes, the subgenera *Paraclivina* Kult, *Semiclivina* Kult, and the *atrata-*, *biplagiata-, brevicornis-, coronata-, coryzoides-, cribrosa-, debilis-, denticollis-, grandiceps-, incerta-, lobata-, obliquata-, obsoleta-, orbitalis-, planicepes-, sulcaticeps-, tranquebarica-,* and *wurargae*-groups of the genus *Clivina* Latreille. With a note on a record of the genus *Parathlibops* Basilewsky (Scapterini) (Carabidae, Scaritinae). *Coleoptera* 12: 1-220.

Balkenohl M. 1999. Revision of the genus *Trilophus* Andrewes from the Oriental region (Coleoptera, Carabidae). *Revue suisse de Zoologie* 106: 429-537.

Balkenohl M. 2001. Key and Catalogue of the tribe Clivinini from the Oriental realm, with revisions of the genera *Thliboclivina* Kult, and *Trilophidius* Jeannel (Insecta, Coleoptera, Carabidae, Scarititae, Clivinini). *Pensoft Series Faunistica* 21. Pensoft Publ., Sofia-Moscow. 83 pp.

Balkenohl M. 2017. Scaritinae (pp. 254-279). *In:* Löbl I. & Löbl D. (Eds), Catalogue of Palaearctic Coleoptera. Volume 1. Revised and Updated Edition. Archostemata, Myxophaga, Adephaga. *Brill: Leiden, Boston*, 1443 pp.

Balkenohl M. 2021a. On the subfamily Scaritinae Bonelli, 1810 from Sri Lanka, with the description of a new species (Coleoptera, Carabidae, Scaritinae). *Linzer biologische Beiträge* 53(1): in press.

Balkenohl M. 2021b. Revision of the *Clivina castanea*-species group from Asia (Coleoptera: Carabidae: Clivinini). *Belgian Journal of Entomology* 115: 1-83.

Basilewsky P. 1948. Carabidae africains nouveaux. I. *Mémoires de la Société entomologique de Belgique* 25: 57-105, plus 1 Tab.

Basilewsky P. 1956. Coléoptères recueillis par N. Leleup au Lac Tumba. I. Carabidae. *Revue de Zoologie et de Botanique Africaines* 53: 418-434.

Basilewsky P. 1959. Sur les genres *Syleter* Andrewes, *Psilidius* Jeannel et *Leleuporella* Basilewsky (Col. Carabidae Scaritinae). *Revue Française d'Entomologie* 26: 5-16.

Bates H.W. 1889. Contributions à la faune Indo-Chinoise. *Annales de la Société entomologique de France* 9: 261-286.

Bonelli F.A. 1810. Observations entomologiques. Première partie (cicindélètes et portion des carabiques). Félix Galletti, Turin, 58 pp., 1 pl.

Bouchard J. 1903. Insectes recueillis par M. le Professeur Dr Forster à Borneo, Java et Sumatra (Palembang). Coléoptères Carabiques. *Annales de la Société entomologique de Belgique* 72: 169-176.

Darlington P.J. 1962. The Carabid beetles of New Guinea Part I. Cicindelinae, Carabinae, Harpalinae through Pterostichini. *Bulletin of the Museum of Comparative Zoology* 126: 321-564.

Dejean P.F.M.A. 1826. Species général des coléoptères, de la collection de M. le Compte Dejean. Tome second. *Paris: Crevot*, viii + 501 pp.

Jeannel R. 1957. Révision des petits Scaritides endogés voisins de *Reicheia* Saulcy. *Revue Française d'Entomologie* 24: 129-212.

Kryzhanovskij O.L. 1976. An attempt at a revised classification of the family Carabidae (Coleoptera). *Entomological Review* 55: 80-91.

Kryzhanovskij O.L. 1983. Beetles of the suborder Adephaga: Family Rhysodidae, Tachypachidae; family Carabidae (introductory part and revision of the fauna SSSR). *Fauna SSSR*, Vol. 1, Part 2. N.S. No. 128: 1-341.

Kult K. 1959. Revision of the African Species of the old genus *Clivina* Latr. (Col. Carabidae). *Revue de Zoologie et de Botanique Africaines* 60: 193-225.

Latreille P.A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et partie du cours complet l'histoire naturelle rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Tome troisième. *F. Dufart*, Paris, xii + pp. 13-467.

Lorenz W. 1998. Systematic list of extant Ground Beetles of the World (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodidae). First Edition, 1998 – *Tutzing, printed by the author*. 502 pp.

Lorenz W. 2005. Systematic list of extant Ground Beetles of the World (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodidae). Second Edition, 2005 – *Tutzing, printed by the author*. 530 pp.

Louwerens C.J. 1953. New Carabidae from the Malay Archipelago. *Zoologische Mededelingen* 32: 87-95.

Moore B.P., Weir A., Pyke J.E. 1987. Carabidae. *In:* Zoological Catalogue of Australia. *Australian Government Publishing Service, Canberra.* 4: 23-443.

Putzeys J.A.A.H. 1846. Monographie des *Clivina* et genres voisins, précédée d'un tableau synoptique des genres de la tribu des Scaritides. *Mémoires de la Société Royale des Sciences de Liège* 2: 521-663.

Putzeys J.A.A.H. 1867. Révision générale des Clivinides. *Annales de la Société Entomologique de Belgique* 10[1866]: 1-242.

Putzeys J.A.A.H. 1868. Supplément à la révision générale des Clivinides. *Annales de la Société Entomologique de Belgique* 11: 7-22.

Putzeys J.A.A.H. 1873. Deuxième supplément à la révision générale des Clivinides. *Annales de la Société Entomologique de Belgique* 16: 10-18.

Putzeys J.A.A.H. 1877. Comptes-rendus des Séances de la Société Entomologique de Belgique. *Annales de la Société Entomologique de Belgique* 20: XL-XLVII.

Rafinesque C.S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. *L'Imprimerie de Jean Barravecchia*, Palerme, 224 pp.

Whitehead D.R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). *Quaestiones Entomologicae* 8: 131-348.

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On the Peruvian *Erigone palustris* Millidge, 1991, with notes on the *psychrophila*-species group (Arachnida: Araneae)

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Abstract: The Peruvian high-altitude spider species *Erigone palustris* Millidge, 1991, a member of the *psychrophila*-species group, is redescribed and illustrated. This species is very similar to the northern European hypoarcto-boreal *E. svenssoni* Holm, 1975, different only in a few minor details of the male palp. A list of the *psychrophila*-species group is presented and its biogeography is discussed.

Keywords: Taxonomy - Erigoninae - species group - distribution.

INTRODUCTION

At present the *Erigone psychrophila* species group (*sensu* Crosby & Bishop, 1928) includes at least 23 species (see Table 1) which mainly occur in the Northern Hemisphere, mostly in the tundra, boreal and montane regions of the Holarctic. Only two species, *E. clavipalpis* Millidge, 1991 and *E. palustris* Millidge, 1991, live in the Southern Hemisphere, in the highlands of the Peruvian Cordilleras (Millidge, 1991). Four conspicuous species in this group share a characteristically long and sabre-shaped process on the ventral surface of the male palpal tibia (SP in Figs 5, 7): *E. svenssoni* Holm, 1975, known from northern Europe, *E. hydrophytae* Ivie & Barrows, 1935 and *E. uintana* Chamberlin & Ivie, 1935, described from Florida and Uta, U.S.A., respectively, and *E. palustris* Millidge, 1991, from Peru.

Quite unexpectedly, a male labeled as *E. svenssoni* was recently found in the spider collection of the Muséum d'histoire naturelle de Genève, Switzerland. This species is known to occur in the taiga and tundra belts of northern Europe, however the specimen examined was collected in the highlands of the Cordilleras of Peru. Such a disjunction would be so unusual that I decided to carefully check if the identification of that male is correct, since at first glance it truly looked like representing the northern European species.

MATERIAL AND METHODS

This paper is based on spider material kept in the Muséum d'histoire naturelle de Genève, Switzerland (MHNG) and in the personal collection of Andrei Tanasevitch, Moscow (CAT). Specimens preserved in 70% ethanol were studied using a MBS-9 stereomicroscope. A Levenhuk C-800 digital camera was used for taking photos. Leg chaetotaxy is presented in a formula, e.g., 2.2.2.1, which refers to the number of dorsal spines on tibiae I-IV. The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus. All measurements are given in mm. Scale lines in the figures correspond to 0.1 mm unless indicated otherwise. Figure numbers are given above the corresponding scale lines, the length they represent is given below them. The terminology of copulatory organs mainly follows that of Merrett (1963) and that of authors mentioned in the abbreviations below.

Abbreviations

a.s.l.	above sea level
DSA	distal suprategular apophysis *sensu* Hormiga (1994)
E	embolus
EM	embolic membrane *sensu* Tanasevitch (2017), not *sensu* Hormiga (1994, 2000)
EP	embolus proper *sensu* Saaristo (1971)
MRA	median radical apophysis (= median tooth *sensu* Crosby & Bishop, 1928)
MRT	mesal radical tooth (= mesal tooth *sensu* Crosby & Bishop, 1928)
PN	posterior notch of radix
PRA	posterior radical apophysis (= posterior tooth *sensu* Crosby & Bishop, 1928)
SP	sabre-shaped process
TmI	position of trichobothrium on metatarsus I.

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Table 1. Composition and distribution of the *Erigone psychrophila*-species group.

	Species	Zoogeographical regions		
		Palaearctic	**Nearctic**	**Neotropics** (only known from Peru)
1	*E. aletris* Crosby & Bishop, 1928	+	+	
2	*E. angela* Chamberlin & Ivie, 1939		+	
3	*E. clavipalpis* Millidge, 1991			+
4	*E. cristatopalpus* Simon, 1884	+	+	
5	*E. denticulata* Chamberlin & Ivie, 1939		+	
6	*E. dentosa* O. Pickard-Cambridge, 1894	+	+	
7	*E. ephala* Crosby & Bishop, 1928		+	
8	*E. hydrophytae* Ivie & Barrows, 1935		+	
9	*E. hypenema* Crosby & Bishop, 1928		+	
10	*E. koshiensis* Oi, 1960	+		
11	*E. malvari* Barrion & Litsinger, 1995	+		
12	*E. ostiaria* Crosby & Bishop, 1928		+	
13	*E. palustris* Millidge, 1991			+
14	*E. paradisicola* Crosby & Bishop, 1928		+	
15	*E. psychrophila* Thorell, 1871	+	+	
16	*E. reducta* Schenkel, 1950		+	
17	*E. svenssoni* Holm, 1975	+		
18	*E. tenuimana* Simon, 1884	+		
19	*E. tirolensis* L. Koch, 1872	+	+	
20	*E. uintana* Chamberlin & Ivie, 1935		+	
21	*E. whitneyana* Chamberlin & Ivie, 1935		+	
22	*E. whymperi* O. Pickard-Cambridge, 1877		+	
23	*E. zheduoshanensis* Song & Li, 2008	+		
	Total species:	10	16	2

Figs 1-4. Photographs of a male of *Erigone palustris* Millidge, 1991 deposited in the MHNG. (1) Habitus, dorsal view. (2-4) Prosoma, dorsal, ventral and frontal views, respectively.

TAXONOMY

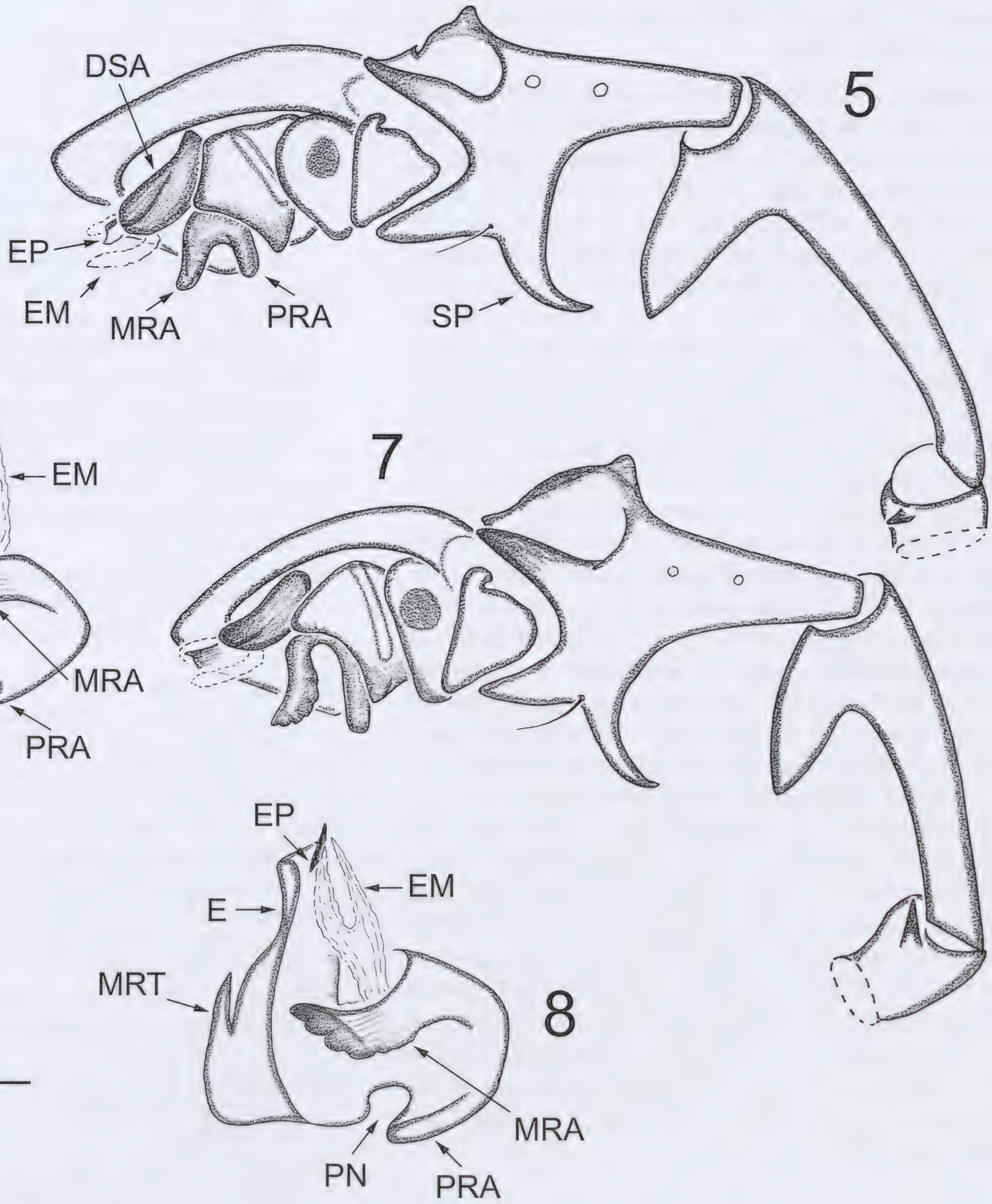
Erigone palustris Millidge, 1991

Figs 1-6

Material: MHNG; 1 male, labeled as *Erigone svenssoni* Holm; PERU, Junin Department, La Oroya, Pachacayo, 3700-3750 m ü NN (= a.s.l.); 22.XII.1978; leg. and det. S. Heimer.

Comparative material examined: *Erigone svenssoni* Holm, 1975: MHNG (collection of S. Heimer); 1 male (see Figs 7-8), 2 females; SWEDEN, Swedish Lapland, Stordalen, mire; 14.-23.VI.1979; leg. Å. Holm. – CAT; 1 male, 6 females; RUSSIA, environs of Vorkuta, near Vorgashor, sedge fen on lake bank; 5.XI.1983; leg. A. Tanasevitch. – CAT; 2 males, 1 female, same locality; 4.IX.1984; leg. A. Tanasevitch.

Description: *Male*. Total length 1.88. Carapace (Figs 1-2, 4) 0.90 long, 0.68 wide, reddish brown, its cephalic part arched. Lateral edges of carapace with irregular sharp teeth of different sizes. Chelicerae 0.50 long, retrolateral-frontal side with a row of small teeth, mastidion absent. Promargin of cheliceral groove with one small and two large teeth, retromargin with two small teeth. Legs yellow. Leg I 2.24 long (0.62 + 0.23 + 0.54 + 0.47 + 0.38), IV, 2.24 long (0.62 + 0.23 + 0.56 + 0.48 + 0.35). Chaetotaxy 2.2.2.1, spines about as long



Figs 5-8. Details of the left palp of a male of *Erigone palustris* Millidge, 1991 (5-6) and of a *E. svenssoni* Holm, 1975 male from Swedish Lapland (7-8) deposited in the MHNG. (5, 7) Palp, retrolateral view. (6, 8) Embolic division, mesal (= prolateral) view.

as diameter of corresponding leg segment. Metatarsus IV without trichobothrium. TmI 0.42. Palp (Figs 5-6): Patella long and slender, with a large, conical ventro-apical apophysis. Tibia elongated, with an anterior concavity typical for the *psychrophila*-species group, and with a characteristic ventral sabre-shaped process. Distal suprategular apophysis elongated, rounded distally, strongly sclerotized. Embolic division typical for the group: mesal radical tooth conical, pointed; median radical apophysis not expanded distally; embolic membrane bipartite, transparent. Posterior notch of radix very small, resulting in a short posterior radical apophysis. Abdomen 1.00 long, 0.68 wide, pale grey.

Distribution: The species is known only from the highlands of the Peruvian Cordilleras at 2530-3850 m a.s.l. (Millidge, 1991).

Remarks: The spider collection of the MHNG has a male labeled as *Erigone svenssoni* Holm, 1975, which has been collected by Stefan Heimer (Dresden) in the highlands of the Peruvian Cordilleras in 1979. In 1991 A.F. Millidge described *E. palustris* on the basis of several males and females from high altitudes (2530-3850 m a.s.l.) from the same mountain region of Peru (Millidge, 1991). In the diagnosis of this species Millidge did not mention that it belongs to the *psychrophila*-species group, and only compared it with a few *Erigone* species known from South America. On the other hand, Heimer was not far from the truth, having identified the male he collected in Peru as the Swedish Laplandic *E. svenssoni*. *Erigone svenssoni* was originally described from Sweden (Holm, 1975) and later also recorded from the northern part of the Russian Plain [Karelia (Byzova *et al.*, 1986)], from the Polar Urals (Esyunin *et al.*, 1995), and from the Bolshezemelskaya tundra (Tanasevitch & Koponen, 2007). Both species belong to the *psychrophila*-species group, and are really very similar to each other. The male from high-altitudes of Peru, belonging to *E. palustris*, differs from that of the northern European hypoarcto-boreal *E. svenssoni* by a few details of the embolic division, i.e. the shorter median radical apophysis with a more or less even apical edge (see MRA in Figs 6, 8), the smaller posterior notch of the radix, and the smaller posterior radical apophysis (see PN and PRA in Figs 6, 8). The epigynes of both species are rather different in the shape of the posterior median plate (triangular in *E. svenssoni vs* trapezium-shape in *E. palustris*) and of the receptacles [much large in the European species (Holm, 1975: fig. 8; cf. Millidge, 1991: fig. 551)].

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REFERENCES

Barrion A.T., Litsinger J.A. 1995. Riceland spiders of South and Southeast Asia. *CAB International, Wallingford, Oxon,* xix + 700 pp.

Byzova Yu.B., Uvarov A.V., Gubina V.T., Zalesskaya N.T., Zakharov A.A., Petrova A.D., Suvorov A.A., Vorobeva E.T. 1986. *Soil Invertebrates of the White Sea Islands of the Kandalaksha Reserve. Nauka, Moscow*, 312 pp. [in Russian]

Chamberlin R.V., Ivie W. 1935. Miscellaneous new American spiders. *Bulletin of the University of Utah* 26(4): 1-79.

Chamberlin R.V., Ivie W. 1939. Studies on North American spiders of the family Micryphantidae (pp. 56-73, pls 1-6). *In*: Jordan K., Hering E.M. (eds), VII. Internationaler Kongress für Entomologie, Berlin, 1938. Verhandlungen, Band 1. *Selbstverlage der Internationalen Kongresse für Entomologie, Weimar,* 617 pp.

Crosby C.R., Bishop S.C. 1928. Revision of the spider genera *Erigone*, *Eperigone* and *Catabrithorax* (Erigoneae). *New York State Museum Bulletin* 278: 1-73.

Esyunin S.L., Efimik V.E., Polyanin A.B. 1995. Remarks on the Ural spider fauna, 5. New records of spider species of the family Linyphiidae from the Urals (Arachnida Aranei). *Arthropoda Selecta* 4(2): 49-71.

Holm Å. 1975. A new species of the genus *Erigone* Sav. & Aud. (Araneae: Erigonidae) from Swedish Lapland. *Entomologisk Tidskrift* 96: 17-23.

Hormiga G. 1994. Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). *Zoological Journal of the Linnean Society* 111: 1-71.

Hormiga G. 2000. Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). *Smithsonian Contributions to Zoology* 609: 1-160.

Ivie W., Barrows W.M. 1935. Some new spiders from Florida. *Bulletin of the University of Utah* 26(6): 1-24.

Koch L. 1872. Beitrag zur Kenntniss der Arachnidenfauna Tirols. Zweite Abhandlung. *Zeitschrift des Ferdinandeums für Tirol und Vorarlberg* (3) 17: 239-328.

Merrett P. 1963. The palpus of male spiders of the family Linyphiidae. *Proceedings of the Zoological Society of London* 140: 347-467.

Millidge A.F. 1991. Further linyphiid spiders (Araneae) from South America. *Bulletin of the American Museum of Natural History* 205: 1-199.

Oi R. 1960. Linyphiid spiders of Japan. *Journal of the Institute of Polytechnics, Osaka City University, series D, Biology* 11: 137-244.

Pickard-Cambridge O. 1877. On some new and little known spiders from the Arctic regions. *Annals and Magazine of Natural History* (4) 20: 273-285.

Pickard-Cambridge O. 1894. Arachnida - Araneidea, vol. 1 (pp. 1-545). *In*: Godman F.D.-C., Salvin O. (eds), Biologia Centrali-Americana. *Taylor & Francis, London*, 610 pp.

Saaristo M.I. 1971. Revision of the genus *Maro* O. P.-Cambridge (Araneae, Linyphiidae). *Annales Zoologici Fennici* 8: 463-482.

Schenkel E. 1950. Spinnentiere aus dem westlichen Nordamerika, gesammelt von Dr. Hans Schenkel-Rudin. Erster Teil. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 61: 28-92.

Simon E. 1884. Les arachnides de France, vol. 5, part 2. *Roret, Paris*, pp. 181-885, pl. 27.

Song Y., Li S. 2008. Four *Erigone* species (Araneae: Linyphiidae) from China. *Revue suisse de Zoologie* 115(3): 451-469.

Tanasevitch A.V. 2017. New species and new records of linyphiid spiders from the Indo-Malayan Region (Araneae, Linyphiidae). *Zootaxa* 4227(3): 325-346.

Tanasevitch A.V., Koponen S. 2007. Spiders of the southern tundra in the Russian Plain. *Arthropoda Selecta* 15(4): 295-345.

Thorell T. 1871. Om Arachnider från Spitsbergen och Beeren-Eiland. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 28: 683-702.

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An exploratory survey and assessment of the hoverfly diversity (Diptera: Syrphidae) from the Pyrenees of Girona, Spain

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Abstract: Syrphidae are pollinators, pest predators and decomposers in European ecosystems. Camprodon (Girona province, Spain) is a valley with rich vegetation and high habitat diversity in the eastern Pyrenees. However, hoverfly biodiversity in this valley was poorly known. To explore the high potential of this area for Syrphidae, a survey with hand-net was undertaken in July/August 2020 in the valley. The list of Syrphidae species from the valley increases to 88, whilst that of the Girona province now extends to 119 species. *Chrysotoxum lessonae* Giglio-Tos, 1890 is reported for the first time from the Iberian Peninsula. The specimens of *Xylota tarda* Meigen, 1822 and *Cheilosia hypena* (Becker, 1894) represent the first documented records of these species for the Iberian Peninsula and Spain, respectively; i.e. these two species were known to occur in the Iberian Peninsula and Spain but without further locality details. A total of 19 species were new to the region of Catalonia and 23 to the Girona province. *Cheilosia* Meigen, 1822 was the genus with the highest number of species recorded, as expected from the combination of mountains, diversity of forest vegetation, and presence of rivers/streams of the Camprodon valley. Faunistic results from this fieldwork are relevant to knowledge of Diptera from Catalonia, a region of Spain where this insect family is understudied.

Keywords: Flowerflies - *Cheilosia hypena* - *Chrysotoxum lessonae* - distribution - Catalonia - Camprodon valley - checklist.

INTRODUCTION

As popular pollinators and pest predators (Rojo *et al.*, 2003; Marshall, 2012; Doyle *et al.*, 2020), Syrphidae are often surveyed at the local scale (e.g. Sommaggio & Corazza, 2006; Sánchez-Heredia *et al.*, 2017; Miličić *et al.*, 2018; Lorenzo *et al.*, 2020). Local surveys are relevant to the understanding of biodiversity in complex ecosystems and contribute to knowledge of regional species lists. Regional lists provide a framework for expert systems to assess the conservation of habitats (Speight & Castella, 2001; Monteil, 2010; Speight *et al.*, 2020).

The massif of the Pyrenees extends east-west over 440 km, forming a natural border between France and Spain, in southwestern Europe. With 19 000 km^2 and a maximum altitude of 3404 m, the Pyrenees are a complex ecosystem with many mountains, U-shaped glaciated valleys, rivers, lakes and a diverse flora and fauna. The Pyrenees can be divided into three parts, Eastern, Central, and Western. North to south, they are divided into the axial or medial Pyrenees, and the pre-Pyrenean or external mountains (Guixé & Llobet, 2016). The north slope of the Pyrenees (France, and the 'Vall d'Aran' in Spain) is more humid, less continental, and with typically Eurosiberian forest, whilst the south slope (Spain) has a Mediterranean influence, with less diverse and more reduced forest (Vázquez & Fernández-Prieto, 2002). In Spain, the Pyrenees are divided into five provinces, with the easternmost part in the Girona province, Catalonia (Ricarte & Marcos-García, 2017).

The studies of Diptera in Catalonia are scattered, both temporally and geographically, and Pyrenean hoverflies are not an exception. Apart from the consequences for our ecological understanding of the Pyrenees, this scattered knowledge has also prevented the popularisation of hoverflies, as shown by their absence from field guides to

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the regional fauna (Guixé & Llobet, 2016). Cuní (1881) was the first to record hoverflies from the Catalonian Pyrenees. Diptera were poorly studied in Catalonia throughout the 20th century (Pujade-Villar, 2011), with only a little fieldwork undertaken in the Pyrenees to collect hoverflies (van Doesburg, 1951; Leclercq, 1971; Lucas, 1976). The 21st century brought new hoverfly records to light from the Catalonian Pyrenees, but most of these were based on specimens collected earlier, usually in the 1970s (Marcos-García *et al.*, 2007, 2011; van Steenis & Lucas, 2011; Ricarte & Nedeljković, 2020). Camprodon is one of the most popular valleys of the eastern Pyrenees, with diverse vegetation and habitats (Sacasas-i-Lluís, 2009). The first hoverfly records from this valley are those of the Rev. José Andreu from 1926. However, just over a dozen species were reported from this valley prior to the present sampling (Andreu, 1926; Gil Collado, 1930; Lucas, 1976; Barkalov & Ståhls, 1997; Marcos-García *et al.*, 2007, 2011; van Steenis & Lucas, 2011; Ricarte & Nedeljković, 2020). The aim of the present study was to improve our knowledge of the hoverflies from the Girona province by undertaking an exploratory survey and faunistic assessment in its Pyrenean part (Camprodon valley) and reviewing all the available literature.

MATERIAL AND METHODS

Study area

Camprodon valley ('Valle de Camprodón' in Spanish) is located in the axial eastern Pyrenees. This hilly valley is in the eastern part of the Ripollès region, Girona province (abbreviated as 'GI' hereinafter), Spain. The climate is typical Pyrenean, humid and rainy. The Ter river, which rises at high altitudes in this valley, is also the main water course in it. All along the valley, there are some scattered small villages and there is a ski resort at about 2000 m asl. The diverse vegetation of the Camprodon valley is dominated by a mosaic of woodlands and grasslands as a result of a long history of human use. The montane and subalpine altitudinal zones are represented in the valley. Montane vegetation (700-1600 m asl) consists mainly of deciduous forest of *Quercus* spp. and *Fagus sylvestris* L., as well as forest of red pine (*Pinus sylvestris* L.). The dominant species in the understory of the montane forest is the common box (*Buxus sempervirens* L.). Montane vegetation of riversides includes *Salix*, *Populus* and *Alnus* trees. Subalpine vegetation (1600-2300 m asl) is dominated by forests of black pine (*Pinus uncinata* Ramond ex A. DC.) that are usually more open at higher altitudes, with alpenrose (*Rhododendron ferrugineum* L.) in the understory. Grasslands are also typical of the subalpine zone (Sacasas-i-Lluís, 2009). The sampling sites of the present study within the Camprodon valley are detailed in Table 1. Sites belong to four different villages, Camprodon, Llanars, Setcases, and Vilallonga de Ter.

Fieldwork and hoverfly identification

Adult hoverflies were collected by Antonio Ricarte and Zorica Nedeljković using hand-nets, from 29 July to 3 August 2020. Vegetation and especially flowers (e.g. *Heracleum sphondylium* L., *Hypericum* sp., *Eupatorium cannabinum* L., *Knautia* sp., *Pastinaca* sp.) were inspected for hoverflies in sunny areas, and also on some hilltops (S3, S14). Specimens were kept in tubes in the freezer until defrosting in the lab for preparation. Specimens were pinned and labelled following the usual techniques (Galante & Marcos-García, 2004). A bar code label was assigned to each specimen and the information databased in an Excel file. Bar code numbers were written for each specimen (as a single code) or series of specimens (as a range of codes) in the examined material. Every code starts with 'CEUA' plus a number of zeros and then the actual code number (e.g. CEUA00050300), but only the number is indicated in the list of examined material.

Specimens were identified to the species level by Antonio Ricarte and Zorica Nedeljković, except otherwise stated. The literature used for identification is Nielsen (1970), Violovitsh (1974), Dušek & Láska (1976), Goeldlin de Tiefenau (1976), Marcos-García & Láska (1983), Vujić (1992), Vujić & Šimić (1995-1998), Goeldlin de Tiefenau (1996), Barkalov & Ståhls (1997), Verlinden (1999), Vujić (1999), van Steenis (2000), Hippa *et al.* (2001), Sommaggio (2001), Claussen & Ståhls (2007), Ståhls *et al.* (2008), Barkalov (2009), Bartsch *et al.* (2009a, b), Ricarte *et al.* (2010), van Veen (2010), van Steenis & Lucas (2011), Nedeljković *et al.* (2013), Vujić *et al.* (2013), Haarto & Ståhls (2014), van Steenis *et al.* (2016), Speight & Sarthou (2017), Vujić *et al.* (2017), Nedeljković *et al.* (2018), and van Steenis *et al.* (2020). When it was necessary to confirm the species identification, male genitalia were dissected with entomological pins. They were cleared in a hot solution of KOH for up to 5 min, immersed in acetic acid to remove excess KOH, washed in 70% alcohol, and stored in microvials containing glycerine. When specimens were dry, they were first relaxed in a humid chamber before genitalia removal. All specimens are deposited in the CEUA-CIBIO collection, University of Alicante, Spain. Hoverflies were photographed in the field by Antonio Ricarte (except where otherwise stated) with a camera Canon® PowerShot SX730 HS. A pinned specimen of *Chrysotoxum* Meigen, 1803 was illustrated (Fig. 1) with photos produced as stacks of individual images made with a camera (Leica DFC 450) attached to a binocular stereomicroscope (Leica M205 C). Stacks were made in Leica Application Suite X (LAS X) ®, v. 3.0.4.16529.

Taxonomic and faunistic assessments

For the collected hoverflies, the faunistic novelty of each species (Appendix) was assessed on the basis

Table 1. Sampling sites in the eastern Pyrenees of Girona province (Spain) during July/August 2020 field work. The dates when each site was visited is also presented.

Site code	Site	Latitude	Longitude	Altitude (m)	Date/s
S1	Camprodon, 'Roureda de can Pascal' and vicinity	42.313253°	2.386996°	975	01.08.2020
S2	Llanars, L'Escón guesthouse	42.321504°	2.343851°	998	29.07.2020
S3	Llanars, La Creueta	42.324524°	2.339819°	1138	29.07.2020
S4	Llanars, riverside of 'la Riera de Feitús', near 'Font del tir', on flowers of *Heracleum sphondylium*	42.329624°	2.346578°	1007	29.07.2020
S5	Llanars, route Llanars-Camprodon, Ter riverside	42.317926°	2.350075°	964	29.07.2020
S6	Setcases, track up to the water store	42.381322°	2.301701°	1317	30.07-02.08.2020
S7	Setcases, Vallter 2000 sky centre	42.422851°	2.267581°	2000-2100	30.07.2020
S8	Setcases, Vall de Querlat, crossroads with the Espinavell track	42.394433°	2.289479°	1460	30.07.2020
S9	Vilallonga de Ter, track to La Abella	42.328649°	2.311320°	1055	03.08.2020
S10	Vilallonga de Ter, Vilallonga-Setcases road, roadside vegetation	42.354237°	2.292147°	1161	
S11	Vilallonga de Ter, 'Ribera de Tregurà' riverside	42.336798°	2.289106°	1157	31.07.2020
S12	Vilallonga de Ter, Ter riverside, near Vilallonga-Setcases road	42.357085°	2.292184°	1166	01-02.08.2020
S13	Vilallonga de Ter, Ribera de Tregurà, on flowers of *Pastinaca* at the roadsides	42.341194°	2.296101°	1113	31.07.2020
S14	Vilallonga de Ter, Tregurà de Dalt, near aerial	42.347625°	2.281892°	1557	31.07.2020

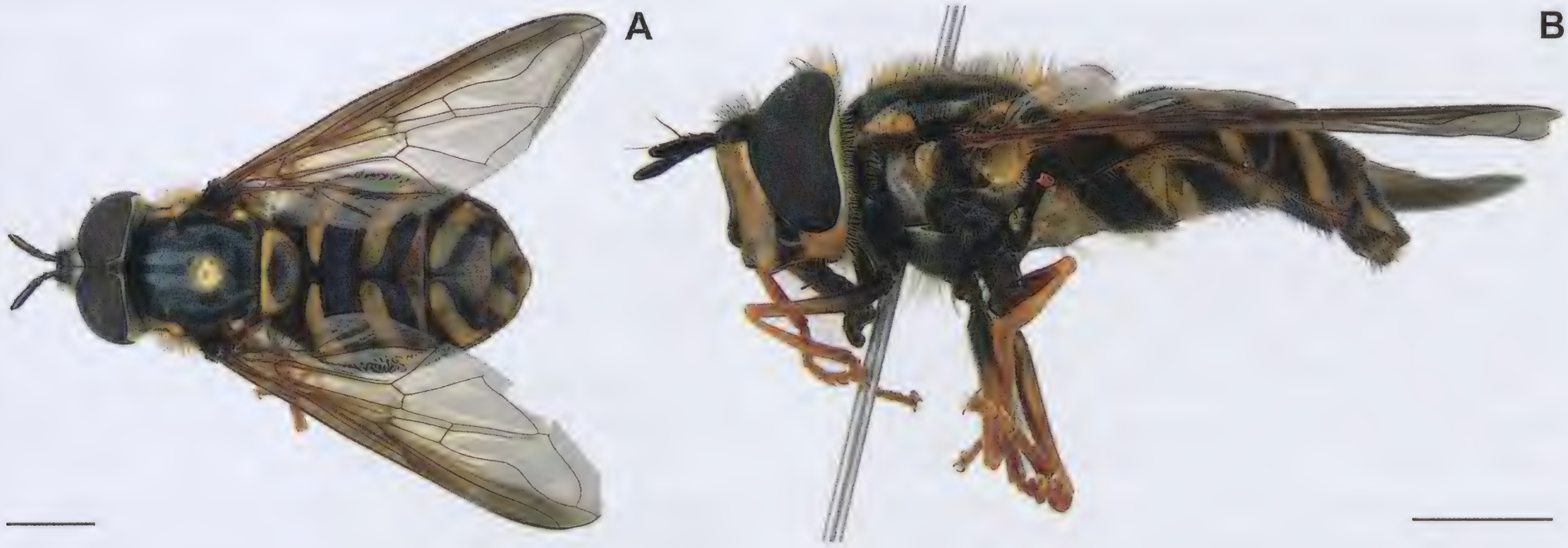

Fig. 1. *Chrysotoxum lessonae* male, from Camprodon valley, Girona province, Spain. (A) Dorsal view. (B) Lateral view. Scale bar = 2 mm.

of Ricarte & Marcos-García (2017) plus all other subsequent faunistic references. The Iberian Peninsula is here interpreted as the unit encompassing the mainland parts of Spain and Portugal together, plus Andorra. First documented records are also indicated in order to make locality details available for those species that had imprecise records in previous literature. A full list of material examined is provided for each species by using the site codes of Table 1. Collection dates are written in the examined material lists only for the specimens caught in S6 and S12, because these sites were visited on more than one day. For the taxonomic classification of the species collected, the arrangement of subfamilies used – indicated after each species name – follows Mengual *et al.* (2015). Genus and species names generally follow Speight (2020).

Checklist of Girona hoverflies

The species collected in this study are also presented in the broader frame of an updated checklist of the hoverflies from Girona province. Localities and references are provided for every species in the checklist. The following localities are listed, based on both literature and the present study: L1, Arbucias; L2, Blanes; L3, Caldes de Malavella; L4, Camprodon; L5, Caralps; L6, Cerdaña; L7, Empalme; L8, Figueras; L9, Flassa; L10, La Bisbal; L11, La Molina; L12, Llanars; L13, Massanas; L14, Massanet de la Selva 'Maçanet-Massanes station'; L15, Mollo; L16, Nuria; L17, Pals; L18, Puigcerdà; L19, Ribas; L20, Ribas de Freser; L21, Rosas; L22, San Cristóbal de Tosas; L23, San Juan de las Abadesas; L24, San Marsal; L25, Sant Ilari de Sacalm; L26, Sarriá; L27, Setcases; L28, Sils; L29, Torroella; L30, Viladrau; L31, Vilallonga de Ter; L32, 'Between Campodron and Setcases'; L33, 13 km south to Girona city. Locality L4 includes the sampling site S1 of the present study; L12 includes S2, S3, S4, S5; L27 includes S6, S7, S8; L31 includes S10, S11, S12, S13, S14 (Table 1).

The following references were reviewed (numbers are used in the checklist to identify each individual reference): 1, Cuní (1880); 2, Cuní (1881); 3, Cuní (1885); 4, Antiga, 1888; 5, Andreu (1926); 6, Gil Collado (1930); 7, Leclercq (1963); 8, Leclercq (1971); 9, Lucas (1974); 10, Lucas (1976); 11, Goeldlin de Tiefenau (1989); 12, Barkalov & Ståhls (1997); 13, Marcos-García *et al.* (2002); 14, Marcos-García *et al.* (2007); 15, van Eck (2010); 16, Marcos-García *et al.* (2011); 17, van Steenis & Lucas (2011); 18, Álvarez-Fidalgo *et al.,* 2018; 19, van Steenis *et al.* (2020); 20, Ricarte & Nedeljković (2020). Marcos-García *et al.* (1998) is not included in the list of references because it does not provide information on the localities within provinces. Dirickx (1994) also omits locality details for species but does provide maps with distribution points, so is not cited in this checklist, except for comments on the distribution of certain species.

Regarding specific references, the following questions should be noted: *a)* Cuní (1881) reported hoverflies from the Spanish Cerdaña, which is divided between the Lleida and Girona provinces and he did not specify where each species was collected. Since he was based on Puigcerdà (Girona) for fieldwork, we assume here that all species belong to GI. *b)* Gil Collado (1930) reports hoverflies from 'Ribas' and 'Rivas', one from Madrid (Rivas?) and other from GI (Ribas? i.e. Ribas de Freser? Ribas valley?), however both names are written as 'Ribas' in the locality index of Gil Collado (1930), and Ribas/ Rivas also appear to be inconsistently used throughout his monograph. Thus, we include Ribas in the present checklist when there were enough grounds to believe that the species was collected in the Ribas of GI.

All species are numbered and presented in alphabetical order, including the species reported in the present work (indicated as 'present study'). Genus and species names in the checklist follow Speight (2020), which can be consulted together with Peck (1988) for authority and year of each taxon. Where species names used in the historical literature under review have been superceded, those are given after the current name and are preceded by (=).

RESULTS

New hoverfly records from the Camprodon valley

Baccha elongata (Fabricius, 1775) (Syrphinae)
Examined material: 108852; 1 male; S5. – 108851; 1 male; S6; 31.07.2020.

Ceriana conopsoides (Linnaeus, 1758) (Eristalinae)
Examined material: 108188; 1 male; S6; 31.07.2020; on flowers of *Heracleum sphondylium*.

Cheilosia aerea Dufour, 1848 (Eristalinae)
Examined material: 108792; 1 male; S6; 31.07.2020.

Cheilosia barbata Loew, 1857 (Eristalinae)
Examined material: 108791, 108790, 108809; 3 males; 108801, 108814, 108816-108818; 5 females; S6; 30.07.2020. – 108804-108808; 5 males; 108800, 108820; 2 females; S6; 31.07.2020. – 108803; 1 male; 108813; female; 02.08.2020. – 108812, 108819; 2 females; S9. – 108811; 1 female; S10.

Cheilosia hypena Becker, 1894 (Eristalinae)
Examined material: 108320; 1 male; S6; 30.07.2020. – 108325-108328; 4 males; S6; 108321-108324; 4 females; S6; 31.07.2020; 108778, 108779; 2 males; S6; 02.08.2020. – 108310; 1 male; 108329; 1 female; S5. – 108777; 1 female; S1. – 108776 (1 female); S11.

Cheilosia illustrata (Harris, 1776) (Eristalinae)
Examined material: 108770; 1 male; 108772, 108789; 2 females; S6; 30.07.2020; on flowers of *Heracleum sphondilium*. – 108771; 1 male; S6; 02.08.2020; on flowers of *Heracleum sphondylium*.

Cheilosia laticornis Rondani, 1857 (Eristalinae)
Examined material: 108785; 1 male; 108784; 1 female; S6; 30.07.2020.

Cheilosia latifrons (Zetterstedt, 1843) (Eristalinae)
Examined material: 108810; 1 female; S6; 30.07.2020. – 108829; 1 female; S6; 02.08.2020; 108828; 1 female; S9. – 108802; 1 female; S1.

Cheilosia longula (Zetterstedt, 1838) (Eristalinae)
Examined material: 08773; 1 male; S11; det. I. Ballester.

Cheilosia proxima (Zetterstedt, 1843) (Eristalinae)
Examined material: 108788; 1 male; S3.

Cheilosia scutellata (Fallén, 1817) (Eristalinae)
Examined material: 108826; 1 male; 108824; 1 female; S5. – 108827, 1 male; S4. – 108825; 1 female; S6; 30.07.2020.

Cheilosia variabilis (Panzer, 1798) (Eristalinae)
Examined material: 108787; 1 female; S6; 30.07.2020. – 108786; 1 female; S7.

Cheilosia vernalis (Fallén, 1817) (Eristalinae)
Examined material: 108794, 108795; 2 males; S6; 31.07.2020. – 108793; 1 female; S12.

Cheilosia vicina (Zetterstedt, 1849) (Eristalinae)
Examined material: 108775; 1 male; S6; 30.07.2020. – 108774; 1 female; S7.

Cheilosia vulpina (Meigen, 1822) (Eristalinae)
Examined material: 108780; 1 male; S3. – 108798; 1 male; S5. – 108797; 1 female; S4. – 108799; 1 male; 108796; 1 female; S13.– 108783, 108782; 2 males; S6; 31.07.2020. – 108781; 1 male; 108802; 1 female; S1; 01.08.2020.

Chrysogaster solstitialis (Fallén, 1817) (Eristalinae)
Examined material: 108234; 1 male; 108269, 108268; 2 females; S3. – 108236; 1 male; 10830-108232, 108240; 4 females; S6; 30.07.2020. – 108237, 108233; 2 males; 10841-108244; 4 females; S6; 31.07.2020; 108235; 1 male; S10. – 108267; 1 female; S9.

Chrysotoxum arcuatum (Linnaeus, 1758) (Syrphinae)
= *Chrysotoxum fasciatum* (Müller, 1764)
Examined material: 108548; 1 female; S6; 31.07.2020.

Chrysotoxum bicinctum (Linnaeus, 1758) (Syrphinae)
Examined material: 108549; 1 male; S11. – 108530; 1 female; S9.

Chrysotoxum elegans Loew, 1841 (Syrphinae)
Examined material: 108546; 1 male; S4; 108547; 1 male; S6; 30.07.2020. – 108545; 1 male; S6; 31.07.2020. – 108544; 1 male; S13.

Chrysotoxum festivum (Linnaeus, 1758) (Syrphinae)
Examined material: 108295; 1 female; S9.

Chrysotoxum lessonae Giglio Tos, 1890 (Syrphinae)
(Fig. 1)
Examined material: 108296-108298; 3 males; S12.

Chrysotoxum volaticum Séguy, 1961 (Syrphinae)
Examined material: 108531; 1 female; S14.

Dasysyrphus albostriatus (Fallén, 1817) (Syrphinae)
Examined material: 108887; 1 female; S11; 108888; 1 male; S12. – 108885; 1 male; 108886; 1 female; S9.

Episyrphus balteatus (de Geer, 1776) (Syrphinae)
Examined material: 108834; 1 female; S5. – 108833; 1 male; S11.

Eristalinus sepulchralis (Linnaeus, 1758) (Eristalinae)
Examined material: 108208; 1 female; S1.

Eristalinus taeniops (Wiedemann, 1818) (Eristalinae)
Examined material: 108206; 1 male; S9.

Eristalis arbustorum (Linnaeus, 1758) (Eristalinae)
Examined material: 108170; 1 male; S13.

Eristalis interrupta (Poda, 1761) (Eristalinae)
= *Eristalis nemorum* Linnaeus, 1758
Examined material: 108211; 1 female; S6; 30.07.2020; 108212; 1 male; 01.08.2020. – 108149; 1 female; S5. – 108210; 1 female; S11. – 108142; 1 female; S12.

Eristalis jugorum Egger, 1858 (Eristalinae)
Examined material: 108152; 1 female; S8. – 108167; 1 male; S6; 30.07.2020. – 108311; 1 male; S6; 02.08.2020. – 108141, 108312, 108313; 3 females; S10.

Eristalis lineata (Harris, 1776) (Eristalinae)
= *Eristalis horticola* (de Geer, 1776)
Examined material: 108133; 1 female; S6; 30.07.2020.

Eristalis pertinax (Scopoli, 1763) (Eristalinae)
(Fig. 2A)
Examined material: 108143, 108144, 108148; 3 males; 108147; 1 female; S4. – 108150, 108216, 108215; 3 males; S1. – 108169; 1 male; S10. – 108158, 108214; 2 males; S6; 30.07.2020. – 108213; 1 male; 108140; 1 female; S6; 02.08.2020.

Fig. 2. Hoverfly species from Camprodon valley, Girona, Spain. (A) *Eristalis pertinax*, male, flowers of *Eupatorium cannabinum*, Setcases. (B) *Ferdinandea cuprea*, female, flowers of *Hypericum* sp., Vilallonga de Ter. (C) *Milesia crabroniformis*, male, Camprodon. Photos A, B by Antonio Ricarte, C by M. Carbonell.

Eristalis similis (Fallén, 1817) (Eristalinae)
Examined material: 108131; 1 male; S3. – 108130; 1 female; S5. – 108145, 108146; 2 males; S4. – 108156; 1 male; 108137; 1 female; S7. – 108134, 108135, 108153, 108157, 108159; 5 males; 108136; 1 female; S6; 30.07.2020. – 108155; 1 male; S6; 31.07.2020. – 108151; 1 female; S1. – 108168; 1 male; S12; 01.08.2020. – 108543; 1 male; S14.

Eristalis tenax (Linnaeus, 1758) (Eristalinae)
Examined material: 108132, 108120; 2 males; S3; 108138; 1 male; 108154; 1 female; S7. – 108139; 1 male; S6; 30.07.2020.

Eumerus grandis Meigen, 1822 (Eristalinae)
Examined material: 108275; 1 male; S6; 30.07.2020. – 108274; 1 male; S6; 02.08.2020.

Eumerus ornatus Meigen, 1822 (Eristalinae)
Examined material: 108229; 1 male; 108222, 108223; 2 females; S12. – 108227; 1 male; 08221; 1 female; S6; 30.07.2020. – 108224-108226, 108228; 4 males; S6; 31.07.2020.

Eupeodes corollae (Fabricius, 1794) (Syrphinae)
Examined material: 108832; 1 male; S7. – 108830, 108831; 2 females; S6; 30.07.2020. – 108849; 1 female; S11. – 108848; 1 female; S9.

Eupeodes luniger (Meigen, 1822) (Syrphinae)
Examined material: 108844; 1 male; S6; 30.07.2020. – 108842, 108843; 2 males; S6; 31.07.2020. – 108841; 1 female; S11. – 108840; 1 male; S9.

Eupeodes latifasciatus (Macquart, 1829) (Syrphinae)
Examined material: 108847; 1 male; S6; 02.08.2020.

Ferdinandea cuprea (Scopoli, 1763) (Eristalinae)
(Fig. 2B)
Examined material: 108204, 108200; 2 males; 108218; 1 female; S12; 02.08.2020. – 108202; 1 female; S1; 01.08.2020; 108201; 1 male; S10. – 108219, 108217; 2 females; S9. – 108203; 1 male; S6; 02.08.2020.

Helophilus pendulus (Linnaeus, 1758) (Eristalinae)
Examined material: 108162; 1 female; S6; 31.07.2020. – 108161; 1 male; S4. – 108160, 108179; 2 males; 108178; 1 female; S5. – 108178; 1 female; S11.

Lapposyrphus lapponicus (Zetterstedt, 1838)
(Syrphinae)
Examined material: 108845; 1 male; S6; 30.07.2020. – 108846; 1 male; S6; 31.07.2020.

Leucozona glaucia (Linnaeus, 1758) (Syrphinae)
Examined material: 108884; 1 female; S6; 30.07.2020; on flowers of *Heracleum sphondylium*. – 108883;

1 female; S6; 31.07.2020; on flowers of *Heracleum sphondylium*.

Melangyna compositarum (Verrall, 1873) (Syrphinae)
Examined material: 108869; 1 female; S6; 31.07.2020.

Melangyna umbellatarum (Fabricius, 1794) (Syrphinae)
Examined material: 108850; 1 female; S10.

Melanostoma mellinum (Linnaeus, 1758) (Syrphinae)
Examined material: 108520; 1 male; S3. – 108523, 108522; 2 females; S2. – 108539; 1 male; 108521; 1 female; S6; 30.07.2020.

Melanostoma scalare (Fabricius, 1794) (Syrphinae)
Examined material: 108538; 1 male; 108533; 1 female; S3. – 108535; 1 male; 108534; 1 female; S5. – 108536, 108537; 2 males; 108532; 1 female; S6; 30.07.2020.

Meligramma cincta (Fallén, 1817) (Syrphinae)
Examined material: 108868; 1 female; S7; 30.07.2020. – 108867; 1 female; S8. – 1088661; 1 female; S6; 31.07.2020.

Meliscaeva auricollis (Meigen, 1822) (Syrphinae)
Examined material: 108863; 1 male; S2. – 108860, 108870, 108878; 3 males; 108861, 108862, 108871, 108876, 108879; 5 females; S6; 30.07.2020. – 108874; 1 female; S6; 31.07.2020. – 108875; 1 female; S6; 01.08.2020. – 108877, 108889; 2 males; S7. – 108873, 108872; 2 females; S8.

Meliscaeva cinctella (Zetterstedt, 1843) (Syrphinae)
Examined material: 108865; 1 female; S7. – 108864; 1 male; S6; 31.07.2020.

Myathropa florea (Linnaeus, 1758) (Eristalinae)
Examined material: 108165; 1 male; 108166, 108164; 2 females; S4. – 108163; 1 male; S6; 30.07.2020. – 108205; 1 male; S1.

Orthonevra nobilis (Fallén, 1817) (Eristalinae)
Examined material: 108263; 1 male; S6; 30.07.2020. – 108265, 108264; 2 males; S6; 31.07.2020.

Paragus haemorrhous Meigen, 1822 (Syrphinae)
Examined material: 108836; 1 male; S12; 02.08.2020. – 108835; 1 male; S6; 30.07.2020.

Paragus pecchiolii Rondani, 1857 (Syrphinae)
Examined material: 108837; 1 male; S12; 02.08.2020.

Paragus tibialis (Fallén, 1817) (Syrphinae)
Examined material: 108821-108823, 108838, 108839; 5 males; S3.

Parasyrphus vittiger (Zetterstedt, 1843) (Syrphinae)
Examined material: 108510, 108524; 2 males; 108525-108529; 5 females; S7.

Pipiza festiva Meigen, 1822 (Pipizinae)
Examined material: 108273; 1 male; S9.

Pipiza noctiluca (Linnaeus, 1758) (Pipizinae)
Examined material: 108272; 1 male; S6; 30.07.2020.

Pipizella viduata (Linnaeus, 1758) (Pipizinae)
Examined material: 108288; 1 male; 108287, 108285, 108284; 3 females; S6; 31.07.2020. – 108286; 1 male; S6; 30.07.2020. – 108282, 108281; 2 males; 108283, 108280, 108299; 3 females; S10.

Platycheirus albimanus (Fabricius, 1781) (Syrphinae)
Examined material: 108515; 1 male; S7. – 108514; 1 male; S6; 30.07.2020. – 108513; 1 male; S6; 02.08.2020. – 108511; 1 female; S13. – 108512; 1 male; S9.

Scaeva dignota (Rondani, 1857) (Syrphinae)
Examined material: 108882; 1 male; S9.

Scaeva pyrastri (Linnaeus, 1758) (Syrphinae)
Examined material: 108516; 1 female; S6; 30.07.2020. – 108518; 1 female; S14. – 108517; 1 female; S9.

Scaeva selenitica (Meigen, 1822) (Syrphinae)
Examined material: 108519; 1 male; S6; 31.07.2020. – 108880; 1 female; S6; 02.08.2020. – 108881; 1 female; S9.

Sericomyia bombiforme (Fallén, 1810) (Eristalinae)
Examined material: 108172, 108171; 2 males; S6; 30.07.2020. – 108180; 1 male; 108181; 1 female; S12, on flowers of *Knautia* sp.; 02.08.2020.

Sphaerophoria scripta (Linnaeus, 1758) (Syrphinae)
Examined material: 108854; 1 female; S2. – 108853; 1 male; S5.

Sphegina elegans Schummel, 1843 (Eristalinae)
Examined material: 108266; 1 male; S10; 01.08.2020.

Spilomyia manicata (Rondani, 1865) (Eristalinae)
Examined material: 108189; 1 male; S6; 30.07.2020; on flowers of *Heracleum sphondilium*.

Syritta pipiens (Linnaeus, 1758) (Eristalinae)
Examined material: 108198, 108199; 2 males; S3; 108197; 1 male; S5.

Syrphus ribesii (Linnaeus, 1758) (Syrphinae)
Examined material: 108315; 1 male; S3; 108316; 1 female; S7. – 108314; 1 female; S6; 02.08.2020.

Syrphus torvus Osten-Sacken, 1875 (Syrphinae)
Examined material: 108302, 108301; 2 males; 108304-108306; 3 females; S7. – 108300, 108317, 108318; 3 males; 108303, 108319; 2 females; S6; 30.07.2020.

Syrphus vitripennis Meigen, 1822 (Syrphinae)
Examined material: 108307; 1 male; S4. – 108308; 1 female; S7. – 108309; 1 female; S13.

Triglyphus primus Loew, 1840 (Pipizinae)
Examined material: See Ricarte & Nedeljković (2020).

Volucella bombylans (Linnaeus, 1758) (Eristalinae)
Examined material: 108177; 1 female; S3.

Volucella inanis (Linnaeus, 1758) (Eristalinae)
Examined material: 108176; 1 male; S6; 31.07.2020. – 108187; 1 male; S6; 01.08.2020. – 108185, 108184; 2 males; S10. – 108186; 1 male; S12; 02.08.2020.

Volucella pellucens (Linnaeus, 1758) (Eristalinae)
Examined material: 108173; 1 male; 108175; 1 female; S8; 108174; 1 female; S6; 31.07.2020. – 108182; 1 female; S12; 02.08.2020.

Volucella zonaria (Poda, 1761) (Eristalinae)
Examined material: 108183; 1 male; S6; 01.08.2020.

Xanthandrus comtus (Harris, 1776) (Syrphinae)
Examined material: 108858, 108859; 2 females; S6; 31.07.2020. – 108857; 1 female; S6; 02.08.2020.– 108856; 1 male; 108855; 1 female; S12; 02.08.2020.

Xanthogramma citrofasciatum (de Geer, 1776) (Syrphinae)
Examined material: 108292; 1 female; S12; 02.08.2020. – 108294, 108293; 2 males; S14.

Xanthogramma dives (Rondani, 1857) (Syrphinae)
Examined material: 108290; 1 male; S10. – 108291; 1 male; S9.

Xylota segnis (Linnaeus, 1758) (Eristalinae)
Examined material: 108191, 108195; 2 males; 108194; 1 female; S6; 31.07.2020. – 108192, 108193; 2 males; S6; 02.08.2020.

Xylota sylvarum (Linnaeus, 1758) (Eristalinae)
Examined material: 108196; 1 male; S6; 31.07.2020.

Xylota tarda Meigen, 1822 (Eristalinae)
Examined material: 108190; 1 female; S9. – 108209; 1 male; S12; 02.08.2020.

Taxonomic and faunistic assessment of the new hoverfly records from Camprodon valley

Excluding the records of *Triglyphus primus* Loew, 1840, which represented the first finding of this genus from Spain (Ricarte & Nedeljković, 2020), one (*Chrysotoxum lessonae*) species is new to the Iberian Peninsula, 19 are new to Catalonia, and 23 to GI. First documented records from Spain and the Iberian Peninsula are given for *Cheilosia hypena* and *Xylota tarda*, respectively, meaning that their presence in Spain and the Iberian Peninsula was previously reported in the literature, but without locality details (Appendix).

A total of 81 hoverfly species of 38 genera were identified. The two main subfamilies (Eristalinae and Syrphinae) had a similar number of genera recorded (16 and 19 respectively). Of all genera, 34 were represented by only 1-3 species, while the genus *Cheilosia* Meigen, 1822 had the highest number of species in the study (13 spp.), followed by *Eristalis* Latreille, 1804 (7 spp.) and *Chrysotoxum* Meigen, 1803 (6 spp.).

Taking into consideration the altitudinal zoning indicated in the study area section and Table 1, most species represented in the study were absent from the subalpine zone, where the only exclusive species was *Parasyrphus vittiger*. All species except *P. vittiger* were found in the montane zone. Twelve species were shared between the two sampled altitudinal zones (Fig. 3).

Hoverfly checklist of the Girona province (Table 2)

See the meaning of the locality and reference codes in the Material and Methods section.

Species	Locality (reference/s)
Baccha elongata = *Bacha obscuripennis* = *Baccha obscuripennis*	L1 (1; 4; 6), L12, L27 (present study)
Ceriana conopsoides	L27 (present study)
Ceriana vespiformis	L19 (6)
Cheilosia aerea	L27 (present study)
Cheilosia albitarsis	L19, L23 (5; 6)
Cheilosia barbata	L27, L32 (present study)
Cheilosia flavipes	L5 (5; 6)
Cheilosia fraterna	L18, L19 (5; 6)
Cheilosia impressa	L19 (5; 6)
Cheilosia hypena	L4, L12, L27, L32 (present study)
Cheilosia illustrata	L27 (present study)
Cheilosia laticornis	L14 (15), L27 (present study)
Cheilosia latifrons	L4, L27, L32 (present study)
Cheilosia longula	L32 (present study)
Cheilosia mutabilis	L17 (7)

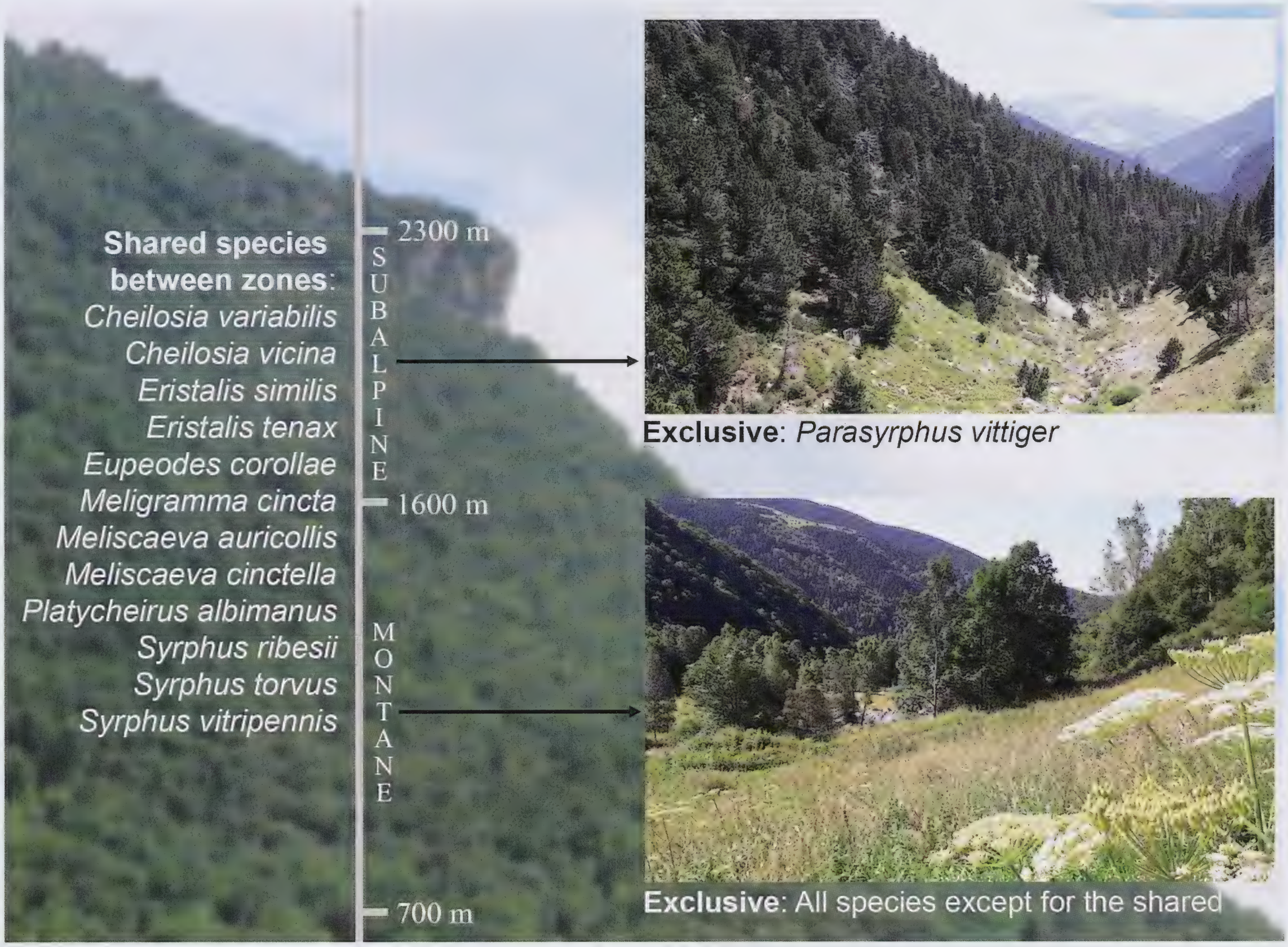

Fig. 3. Distribution of hoverfly species by altitudinal zones (subalpine and montane) from the catch in Camprodon valley, eastern Pyrenees (Spain) in July/August 2020. For each zone, an on-site picture of the representative landscape/vegetation is shown. Species shared between zones are listed on left. Species exclusive of each zone on right.

Species	Locality (reference/s)
Cheilosia personata	L32 (12)
Cheilosia proxima	L12 (present study)
Cheilosia scutellata	L7 (3; 4; 6), L12, L27 (present study)
Cheilosia soror	L14 (15), L19 (5)
Cheilosia variabilis	L27 (present study)
Cheilosia vernalis	L27 (present study), L31 (5; 6), L32 (present study)
Cheilosia vicina	L27 (present study)
Cheilosia vulpina	L12 (present study), L19 (5; 6), L27, L32 (present study).
Chrysogaster coemiteriorum = *Chrysogaster chalybeata*	L1 (4), L27 (5; 6)
Chrysogaster solstitialis	L1, L6 (6), L12, L27, L32 (present study) *Notes*. Cuní (1880, 1881) listed *C. coemiteriorum* from Arbucias and Cerdaña, but Gil Collado (1930) listed instead *C. solstitialis* from these two localities, and *C. coemiteriorum* (as *C. chalybeata*) only from Setcases. Here, we follow Gil Collado (1930) until Cuní's material can be studied.
Chrysotoxum arcuatum	L27 (present study)
Chrysotoxum bicinctum	L27 (19), L32 (present study)
Chrysotoxum elegans	L12, L27, L32 (present study)
Chrysotoxum festivum	L32 (present study)
Chrysotoxum intermedium	L8 (8)
Chrysotoxum lessonae	L32 (present study)

Species	Locality (reference/s)
Chrysotoxum volaticum	L15, L20, L25 (19), L32 (present study)
Dasysyrphus albostriatus = *Syrphus albostriatus* var. *confusus*	L31 (5; 6), L32 (present study)
Episyrphus balteatus = *Syrphus balteatus*	L12 (present study), L17 (7), L21 (3), L32 (present study)
Eristalinus aeneus = *Eristalis aeneus* = *Eristalis (Lathyrophthalmus) aeneus*	L21 (3), L8 (8), L19, L21 (6)
Eristalinus sepulchralis = *Eristalis sepulchralis*	L4 (present study), L9, L10, L29 (7)
Eristalinus taeniops	L32 (present study)
Eristalis arbustorum	L6 (2), L32 (present study), L34 (8)
Eristalis lineata = *Eristalis horticola*	L4 (6), L27 (present study), L31 (5; 6)
Eristalis interrupta	L12, L27, L32 (present study)
Eristalis jugorum	L27, L32 (present study)
Eristalis pertinax	L4, L12, L32 (present study)
Eristalis similis	L4, L12, L27, L32 (present study)
Eristalis tenax	L1 (1), L12 (present study), L3 (3), L6 (2), L27 (present study)
Eumerus grandis	L27 (present study)
Eumerus ornatus	L27, L32 (present study)
Eumerus ovatus = *Eumerus bicolor*	L24 (4; 6)
Eumerus sogdianus	L20, L32 (9)
Eupeodes corollae = *Syrphus corollae* var. *fulvifrons*	L27, L32 (present study), L31 (5; 6)
Eupeodes latifasciatus	L27 (present study) *Notes*. Marcos-García *et al.* (1998) also reports this species from the province of Girona as a pers. com. of Levy.
Eupeodes luniger = *Syrphus luniger*	L4 (6), L27 (present study), L31 (5), L32 (present study) *Notes*. Although this species was reported from Viladrau by Andreu (1926), Gil Collado (1930) omits this record for reasons unknown to us.
Ferdinandea cuprea	L4, L27, L32 (present study)
Helophilus trivittatus	L10 (7), L19 (6)
Helophilus pendulus	L12, L27, L32 (present study)
Lapposyrphus lapponicus	L27 (present study)
Lejogaster metallina = *Chrysogaster (Liogaster) metallina*	L6 (2; 6)
Lejogaster tarsata = *Chrysogaster splendidus* = *Chrysogaster (Liogaster) splendida*	L3 (3; 4; 6)
Leucozona glaucia	L27 (present study), L30 (18)
Melangyna compositarum	L27 (present study)
Melangyna umbellatarum	L32 (present study)
Melanostoma mellinum = *Melanostoma mellina*	L1 (1; 6), L3, L21 (3; 6), L6 (2; 6), L12, L27 (present study)
Melanostoma scalare = *Melanostoma gracilis*	L1 (1; 6), L6 (2; 6), L12, L27 (present study), L31 (5; 6)
Meligramma cincta	L27 (present study)
Meliscaeva auricollis	L12, L27 (present study)
Meliscaeva cinctella	L27 (present study)
Merodon avidus A sensu Marcos-García *et al.* (2007)	L13 (14)
Merodon clavipes	L24 (4)
Merodon funestus	L33 (14)
Merodon rufus	L5, L20, L27 (16)
Merodon unguicornis	L27 (14)
Milesia crabroniformis (Fig. 2C)	L1 (1; 4), L4 (present study)
Myathropa florea = *Helophilus floreus* = *Myiatropa florea*	L3 (3; 6), L4 (present study), L6 (2; 6), L12 (present study), L17 (7), L27 (present study), L31 (5)
Neoascia podagrica	L19 (6)
Orhtonevra nobilis	L27 (present study)
Paragus albifrons	L1 (1; 4; 6)
Paragus haemorrhous = *P. tibialis* var. *triangu-liferus*	L31 (5; 6), L32 (present study)
Paragus pecchiolii = *P. majoranae*	L8 (13), L32 (present study)
Paragus strigatus	Unknown. *Notes*. Marcos-García *et al.* (1998) reports this species from the province of Girona as a pers. com. of Levy. The record from Palafolls (Barcelona province) by van Eck (2010) is here excluded, because it was incorrectly linked to the Girona province.
Paragus tibialis	L1 (1; 6), L4 (6), L12 (present study), L21 (3; 6)
Parasyrphus vittiger	L27 (present study)
Pipiza festiva	L32 (present study)
Pipiza noctiluca	L27 (present study)
Pipizella annulata	L16 (17)
Pipizella brevis	L16 (9; 17)
Pipizella pennina = *Pipizella microapicalis*	L15, L27, L32 (9; 17)

Species	Locality (reference/s)
Pipizella viduata	L27, L32 (present study)
Pipizella zeneggenensis = *Pipizella lata*	L4, L11, L18, L22 (10), L27 (10; 17), L32 (10)
Platycheirus albimanus	L27, L32 (present study)
Platycheirus ambiguus = *Melanostoma ambigua* = *Melanostoma ambiguum*	L3 (3; 6)
Platycheirus fulviventris	Unknown. *Notes*. Marcos-García *et al.* (1998) reports this species from the province of Girona as a pers. com. of Levy.
Platycheirus manicatus	L16 (5; 6)
Riponnensia splendens = *Chrysogaster splendens*	L31 (5; 6)
Scaeva dignota	L32 (present study)
Scaeva pyrastri = *Catabomba pyrastri* = *Lasyophticus pyrastri* = *Syrphus pyrastri*	L5 (5; 6), L6 (2; 6), L27, L32 (present study), L34 (8)
Scaeva selenitica = *Catabomba selenitica* = *Lasyophticus seleniticus*	L27 (present study), L31 (5; 6), L32 (present study)
Sericomyia bombiforme	L27, L32 (present study)
Sphaerophoria interrupta = *Melithreptus menthastri* = *Sphaerophoria menthastri*	L1 (1; 6), L6 (2; 4; 6)
Sphaerophoria laurae	L5, L16 (11)
Sphaerophoria rueppellii = *S. flavicauda*	L17 (7), L31 (5; 6)
Sphaerophoria scripta = *Melithreptus scriptus* = *S. scripta* (var. *nigricoxa,* var. *nitidicollis,* var. *scripta*)	L9 (7), L12 (present study), L17 (7), L21 (3), L26, L29, (7), L31(5), L34 (8)
Sphaerophoria taeniata = *Melithreptus taeniatus* = *Sphaerophoria menthastri* var. *taeniata*	L6 (2; 6)
Sphegina elegans	L32 (present study)
Spilomyia manicata	L27 (present study)
Syritta pipiens	L1 (1), L6 (2), L12 (present study)
Syrphus excisus	L19 (6), L28 (5)
Syrphus ribesii	L6 (2; 6), L12, L27 (present study)
Syrphus torvus	L27 (present study)
Syrphus vitripennis = *S. ribesii* var. *vitripennis*	L12 (present study), L27 (present study), L31 (5; 6), L32 (present study)
Triglyphus primus	L27 (20)
Volucella bombylans = *V. bombylans* var. *plumata*	L12 (present study), S27 (5; 6)
Volucella elegans	L31 (6)
Volucella inanis	L6 (2; 6), L27 (present study), L31 (5; 6), L32 (present study)
Volucella pellucens	L27, L32 (present study)
Volucella zonaria	L1 (1), L3 (3), L6 (2), L27 (present study)
Xanthandrus comtus	L27, L32 (present study)
Xanthogramma citrofasciatum = *Xanthogramma festiva*	L4 (6), L32 (present study)
Xanthogramma dives	L2 (14), L32 (present study). *Notes*. For this species, we follow the criteria of Ricarte & Marcos-García (2017), who consider as valid only the identifications of *X. dives* after Speight & Sommaggio (2010).
Xylota segnis	L27 (present study)
Xylota sylvarum	L27 (present study)
Xylota tarda	L32 (present study)

Doubtful records

Platycheirus europaeus Goeldlin de Tiefenau, Maibach & Speight, 1990
Notes. Speight (2020) states that *P. europaeus* is present in Spain, without further precision. Dirickx (1994) provides a distribution map for this species with a presence dot in Catalonia, but the position of this dot is also imprecise.

Sphegina clavata (Scopoli, 1763) & *Sphegina clunipes* (Fallén, 1816)
Notes. Thompson & Torp (1986) and Dirickx (1994) each provide a distribution map with a presence dot in Catalonia for these two species. The position of this dot is imprecise, but is likely to be within the province of Girona.

Sphegina elegans
Notes. Thompson & Torp (1986) provide a distribution map with a presence dot in Catalonia, very close to the French/Spanish border, and apparently in the Girona province. However, Dirickx (1994) provides a different map without the above-mentioned dot, but with another dot clearly placed on the French side of the Pyrenees. Provenance data for examined material would be necessary to discern whether the dots in Thompson & Torp (1986) and Dirickx (1994) are the same or not.

DISCUSSION

As a result of this short survey in the Camprodon valley, 81 hoverfly species were identified, including *T. primus,* the discovery of which was reported by Ricarte & Nedeljković (2020). The number of known species to this valley now stands at 85, plus *Milesia crabroniformis* (Fabricius, 1775), which is known to the authors of the present paper by a photo taken in Camprodon, on 4 October 2020, by M. Carbonell (Fig. 2C). In addition,

there are also records of a species of *Merodon* Meigen, 1803 and a species of *Rhingia* Scopoli, 1763 collected in the course of this fieldwork but not included in the Results because they are still under taxonomic scrutiny (Ricarte *et al.,* in prep.). In total, 88 species are known for the Camprodon valley. The checklist of hoverflies from the Girona province expands from 73 to 119 species as a result of the new records from Camprodon valley. Girona is now one of the best-known Spanish provinces in terms of number of hoverfly species recorded (Ricarte & Marcos-García, 2017).

Leclercq (1971) provided records of 49 hoverflies collected in the Pyrenees, mainly of the Huesca province, from July/August, i.e. the same period of the year when our sampling took place. More than half (55%) of the species reported by Leclercq (1971) and all genera were shared with our 2020 list. *Cheilosia* was the genus with the highest number of species reported by Leclercq (1971). From the seven *Cheilosia* species reported by him, just one was shared with the 2020 sampling in Camprodon. On the one hand, differences in species composition might be due to the fact that many species of Leclercq (1971) were collected in early July, whilst the 2020 sampling was in late July. On the other hand, detected differences in species composition may actually respond to differences between the surveyed Pyrenean valleys and habitats of Huesca and Girona. Specifically, *Cheilosia* hoverflies are known to be sensible to changes in the woodland landscape (Popov *et al.*, 2017), in part because their larvae, according to species, feed on different plants and fungi (Rotheray, 1993).

From the 81 species reported from the Camprodon valley in 2020, eight were saproxylic, i.e. with larvae dependent on trees (*Ceriana* Rafinesque, 1815, *Ferdinandea* Rondani, 1844, *Myathropa* Rondani, 1845, *Sphegina* Sack, 1928, *Spilomyia* Meigen, 1803, and *Xylota* Meigen, 1822). The proportion of saproxylic species (11%) is unexpectedly low from the Camprodon valley, where forests form a significant element of the vegetation. Although the present study only provides a partial overview of the hoverfly biodiversity of the Camprodon valley, we suggest that land use changes due to the expansion of urban areas and the road network, as well as promotion of agricultural and tourism activities may have had an effect in the woodlands of this popular valley, with reduction of forest cover (mainly in the lower parts of the valley, and around the ski resort), and mature trees becoming scarcer and more isolated; mature trees are crucial for the development of a rich saproxylic community (Micó, 2018).

Hoverfly genera with aquatic larvae such as *Eristalis* Latreille, 1804 (Rotheray, 1993) appear to flourish in the montane ecosystem of the valley (e.g. 7 species of *Eristalis*), where water courses are abundant and water flow is slower than at higher altitudes. In these conditions, breeding sites for *Eristalis* are abundant. However, in the subalpine zone, only *Eristalis similis* and the cosmopolitan *Eristalis tenax* were reported, possibly due to the lower availability of breeding sites in this altitudinal zone of the valley. In the subalpine zone, water courses are smaller and their water flow is faster, due to steeper slopes (pers. obs. of Antonio Ricarte). The only hoverfly species found exclusively in the subalpine was *P. vittiger* (Fig. 3), being in accordance with its preferred environment, the conifer forest, which is dominant at these altitudes (Sacasas-i-Lluís, 2009). The larva of *P. vittiger* feeds mainly on conifer aphids and this is why its presence is correlated with conifers. Nonetheless, *P. vittiger* can occasionally be found in deciduous forest (Speight, 2020).

The genus with the highest number of species found was *Cheilosia*. Hoverflies of this genus prefer mountains, forests and the proximity of rivers and streams (Vujić, 1996), just as in the Camprodon valley. The only species of *Cheilosia* found in the subalpine zone were *C. variabilis* and *C. vicina*, both already recorded from the Pyrenees of Huesca province (Leclercq, 1971; Marcos-García, 1985). The species *C. vicina* belongs to the subgenus *Nigrocheilosia* Shatalkin, 1975, which is typical of high altitudes (Vujić, 1996). *Cheilosia variabilis* is an abundant species in southern parts of its range and occurs in a wide variety of forest types (Vujić, 1996). In addition, the presence of *Cheilosia hypena* is here confirmed from the Spanish Pyrenees. Speight (2020) mentioned that this species was present in this massif but there was no published record from Spain known to us. The finding of *Cheilosia proxima* is also important from a faunistic point of view. Séguy (1961) indicated that this species was present in Catalonia, but without further precision. Apart from this, the only published records of *C. proxima* known to us are from the León and Guipúzcoa provinces (Marcos-García, 1989, 1990a, b; Kehlmaier, 2002). Records of other *Cheilosia* species such as *C. vulpina*, which were previously reported only from 4-5 provinces of Spain (Ricarte & Marcos-García, 2017), are also important to better understand the true distribution of these species in the Iberian Peninsula.

Even though the 2020 sampling was short, faunistic results were remarkable in comparison with studies using longer periods of hand-net sampling in other parts of Spain. For example, in Cabañeros National Park, 82 species were collected by hand-netting during 468 hours of sampling in 13 months (Ricarte & Marcos-García, 2008). The reasons for such a similar result after such different sampling efforts might be due to the sampling designs, which resulted from different research aims, but could also be due to an effect of the diversity of the hoverfly community in each study area. Nonetheless, the results presented here suggest that short surveys conducted by experienced collectors during periods of high insect activity may suffice in the purpose of rapidly evaluating the biodiversity interest of a poorly studied area and/or for taking quick conservation decisions in threatened ecosystems or insect groups with well known

requirements. Further fieldwork in other periods of the year are necessary to complete the inventory of species present in the biodiverse Camprodon valley.

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REFERENCES

Álvarez-Fidalgo M., Álvarez-Fidalgo P., Ricarte A., Marcos-García M. A. 2018. The genus *Leucozona* Schiner, 1860 on the Iberian Peninsula, including the first records of *Leucozona laternaria* (Müller, 1776) (Diptera: Syrphidae). *BV News Publicaciones Científicas* 7(98): 128-141.

Andréu J. 1926. Notas dipterológicas. Una lista de Sírfidos para contribuir al conocimiento de los dípteros de España. *Boletín de la Sociedad entomológica de España* 9(5): 98-126.

Antiga P. 1888. Contribución a la Fauna de Cataluña. Catálogo de los Dípteros observados en diferentes sitios del Principado. *Imprenta de Viuda e Hijos de J. Subirana, Barcelona*, 16 pp.

Barkalov A. 2009. A Key to Hover Flies of the Genus *Cheilosia* Mg. (Diptera, Syrphidae) of Kazakhstan. *Entomological Review* 89(9): 1157-1176.

Barkalov A.V., Ståhls G.1997. Revision of the Palaearctic bare-eyed and black-legged species of the genus *Cheilosia* Meigen (Diptera, Syrphidae). *Acta Zoologica Fennica* 208: 1-74.

Bartsch H., Binkiewicz E., Rådén A., Nasibov E. 2009a. Blomflugor: Syrphinae. Nationalnyckeln till Sveriges flora och flora, DH53a. *Artdatabanken, SLU, Uppsala,* 406 pp.

Bartsch H., Binkiewicz E., Klintbjer A., Rådén A., Nasibov E. 2009b. Blomflugor: Eristalinae & Microdontinae. Nationalnyckeln till Sveriges flora och flora, DH 53b. *Artdatabanken, SLU, Uppsala*, 478 pp.

Becker T. 1894. Revision der Gattung *Chilosia* Meigen. *Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* 62(3): 194-521.

Claussen C., Ståhls G. 2007. A new species of *Cheilosia* Meigen from Thessaly/Greece, and its phylogenetic position (Diptera: Syrpidae). *Volucella* 8: 45-62.

Cuní M. 1880. Excursión entomológica y botánica a San Miguel de Fay. *Anales de la Sociedad Española Historia Natural* 9: 204-242.

Cuní M. 1881. Excursión entomológica y botánica á la Cerdaña Española (Cataluña). *Anales de la Sociedad Española de Historia Natural* 10: 367-389.

Cuní M. 1885. Excursión entomológica a varias localidades de la provincia de Gerona. *Acta de la Sociedad espanola de Historia Natural* 14: 51-73.

de Geer C. 1776. Mémoires pour servir à l'histoire des insectes. *P. Hesselberg, Stockholm*. Vol. 6, viii + 523 pp., 30 pls.

Dirickx H.G. 1994. Atlas des Diptères syrphides de la région méditerranéenne. *Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel,* 317 pp.

Doyle T., Hawkes W.L.S., Massy R., Powney G.D., Menz M.H.M., Wotton K.R. 2020. Pollination by hoverflies in the Anthropocene. *Proceedings of the Royal Society B* 287: 20200508.

Dufour L. 1848. Histoire des Métamorphoses du *Cheilosia aerea*. *Annales des Sciences Naturelles, Zoologie* (3) 9: 205-209.

Dušek J., Láska P. 1976. European species of *Metasyrphus*: key, descriptions and notes. *Acta Entomologica Bohemoslovaca* 73: 263-282.

Egger J. 1858. Dipterologische Beiträge. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich* 8: 701-716.

Fabricius J.C. 1775. *Systemaentomologiae, sistensinsectorumclasses, ordines, genera, species, adiectissynonymis, locis, descriptionibus, observationibus*. Kortii, Flensbvrgiet Lipsiae [= Flensburg & Leipzig]. [32] + 832 pp.

Fabricius J.C. 1781. *Species insectorum. Vol. 2,* C. E. Bohnii, Hamburgi et Kilonii [= Hamburg and Kiel], 494 pp.

Fabricius J.C. 1794. *Entomologia systematica emendata etaucta*. C. G. Proft, Hafniae [= Copenhagen], Vol. 4, [6] + 472 + [5] pp.

Fallén C.F. 1810. *Specim. entomolog. novam Diptera disponendi methodum exhibens*. Berlingianis, Lund. 26 pp.

Fallén C.F. 1816-1817. *Syrphici Sveciae. Berlingianis, Lundae [= Lund],* 1-14 [08.06.1816], 15-22 [08.06.1816], 23-30[10-05.1817], 31-42 [20.05.1817], 43-54 [21.05.1817], 55-62 [22.05.1817] pp.

Galante E., Marcos-García M.A. 2004. Métodos de preparación y conservación (pp. 47-54). *In*: Barrientos J.A. (ed). Curso práctico de entomología. *Manuals de la Universitat Autònoma de Barcelona, Barcelona*, 947 pp.

Giglio-Tos E. 1890. Le specie europee del genere *Chrysotoxum* Meig. *Atti della R. Accademia delle Scienze di Torino* 26: 134-165.

Gil-Collado J. 1930. Monografía de los Sírfidos de España. *Trabajos del Museo Nacional de Ciencias Naturales (Serie Zoológica)*, 54, 376 pp.

Goeldlin de Tiefenau P. 1976. Révision du genre *Paragus* (Dipt., Syrphidae) de la région paléarctique occidentale. *Bulletin de la Société Entomologique Suisse* 49: 79-108.

Goeldlin de Tiefenau P. 1989. Sur plusieurs espèces de *Sphaerophoria* (Dipt., Syrphidae) nouvelles ou méconnues des régions paléarctique et néarctique. *Bulletin de la Société Entomologique Suisse* 62: 41-66.

Goeldlin de Tiefenau P. 1996. On several new European species of *Syrphus* (Diptera, Syrphidae) and key for the Palearctic species of the genus. *Bulletin de la Société Entomologique Suisse* 69: 157-171.

Goeldlin de Tiefenau P., Maibach A., Speight M.C.D. 1990. Sur quelques espèces de *Platycheirus* (Diptera: Syrphidae) nouvelles ou méconnues. *Dipterist's Digest* 5: 19-43

Guixé D., Llobet T. 2016. Vida salvaje de los Pirineos. *Gallocanta ediciones*, 143 pp.

Haarto A., Ståhls G. 2014. When mtDNA COI is misleading: congruent signal of ITS2 molecular marker and morphology for North European *Melanostoma* Schiner, 1860 (Diptera, Syrphidae). *ZooKeys* 431: 93-134.

Harris M. 1776-1780. An exposition of English insects...Robson Co., London, 1776. Decad I, pp. 1-40, 2 pls + pls 1-10 [1776]; Decad II, pp. 41-72, pls 11-20[1778]; Decads III, IV, pp. 73-99, 100-138, pls 21-30, 31-40 [after 24.12.1779]; Decad V, pp. 139-166, pls 41-50+ 1 pl. [1780].

Hippa H., Nielsen T., van Steenis J. 2001. The West Palaearctic species of the genus *Eristalis* Latreille (Diptera, Syrphidae). *Norwegian Journal of Entomology* 48: 289-327.

Kehlmaier C. 2002. Hoverflies (Diptera, Syrphidae) from northern Spain, with notes on *Pelecocera tricincta* Meigen, 1822. *Volucella* 6: 139-153.

Latreille P.A. 1804. Tableau méthodique des insectes [pp. 129-200]. *In:* Latreille P.A. (ed.). Société de Naturalistes et d'Agriculteurs, Nouveau dictionnaire d'histoire naturelle... Tome 24. [Section 3]: *Tableaux méthodiques d'histoire naturelle. Deterville, Paris*, 84 + 4 + 85 + 238 + 18 + 34 pp.

Leclercq M. 1963. Syrphidae de España (Diptera). *Graellsia* 20: 125-129.

Leclercq M. 1971. Syrphidae (Diptera) des Pyrénées (Huesca, Lérida, Andorra, Gerona). *Pirineos* 102: 21-25.

Linnaeus C. 1758. *Systema naturae*. Ed. 10, Vol. 1. 824 pp. L. Salvii, Holmiae [= Stockholm].

Loew H. 1840. Bemerkungen über die in der Posener Gegend einheimischen Arten mehrerer Zweiflugler = Gattungen. *[Zu der] offentlichen Prufung der Schuler des Koniglichen Friedrich-Wilhelms-Gymnasiums zu Posen*, 40 pp.

Loew H. 1841. Ueber die Gattung *Chrysotoxum*. *Stettiner Entomologische Zeitung* 2: 136-141, 155-160.

Loew H. 1857. Die europäischen Arten der Gattung *Cheilosia*. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich (Abhandl.)* 7: 579-616.

Lorenzo D., Ricarte A., Nedeljković Z., Nieves-Aldrey J.L., Marcos-García M.A. 2020. Hoverflies (Diptera: Syrphidae) of El Ventorrillo Biological Station, Madrid province, Spain: a perspective from a late twentieth century inventory. *Revue suisse de Zoologie* 127(2): 393-412.

Lucas J.A.W. 1974. Syrphiden in de jaren 1969-1972. *Entomologische Berichten* 34: 48-51.

Lucas J.A.W. 1976. New species of the genus *Pipizella* Rondani, 1856 (Diptera, Syrphidae). Pubicatiës van het natuur-historisch gennootschap in Limburg, Maastricht 26: 5-13.

Macquart P.J.M. 1829. Insectes diptères du nord de la France. *Syrphies*, Lille. «1827» 223 pp., 4 pls.

Marcos-García M.A. 1985. Contribución al conocimiento de la sirfidofauna del Pirineo del Alto Aragón I (Diptera, Syrphidae). *Boletim da Sociedade Portuguesa de Entomologia (Actas do II Congresso Iberico de Entomologia)* 1: 511-520.

Marcos-García M.A. 1989. Nuevas species de *Cheilosia* (Meigen, 1822) para la entomofauna ibérica (Diptera, Syrphidae). *Fragmenta Entomologica* 21(2): 145-151.

Marcos-García M.A. 1990a. Catálogo preliminar de los Syrphidae (Diptera) de la Cordillera Cantábrica (España). *Eos* 66: 81-235.

Marcos-García M.A. 1990b. El género *Cheilosia* Meigen, 1822, en la Cordillera Cantábrica (Diptera: Syrphidae). *Mediterránea, Serie de Estudios Biológicos* 12: 113-138.

Marcos-García M.A., Láska P. 1983. Description of *Metasyrphus lucasi* sp.n. (Diptera, Syrphidae). *Nouvelle Revue d'Entomologie* 13(1): 113-116.

Marcos-García M.A., Isidro P.M., Rojo S., Pérez-Bañón C. 1998. Catálogo y distribución geográfica de los sírfidos iberobaleares (Diptera, Syrphidae) I.- Syrphinae y Microdontinae. *Boletín de la Asociación española de Entomología* 22(3-4): 37-61.

Marcos-García M.A., Rojo S., Pérez-Bañon C. 2002. Family Syrphidae (pp. 132-136). *In*: Monografías S.E.A. Sociedad Entomológica Aragonesa (ed.). Catálogo de los Dípteros de España, Portugal y Andorra (Insecta). *Sociedad Entomológica Aragonesa (SEA), Zaragoza*, VIII+ 323 pp.

Marcos-García M.A., Vujić A., Mengual X. 2007. Revision of Iberian species of the genus *Merodon* (Diptera: Syrphidae). *European Journal of Entomology* 104: 531-572.

Marcos-García M.A., Vujić A., Ricarte A., Ståhls G. 2011. Towards an integrated taxonomy of the *Merodon equestris* complex (Diptera: Syrphidae) including description of a new species, with additional data on Iberian *Merodon*. *Canadian Entomologist* 143: 332-348.

Marshall S.A. 2012. Flies: the natural history and diversity of Diptera. *Firefly Books Ltd, USA and Canada*, 616 pp.

Meigen J.W. 1803. Versuch einer neuen Gattungs-Eintheilung der europäischen zweiflügeligen Insekten. *Magazin für Insektenkunde* 2: 259-281.

Meigen J.W. 1822. Systematische Beschreibung der bekannten europaischen zweiflügeligen Insekten. *Dritter Theil. Schulz-Wundermann, Hamm.* x + 416 pp., pls 22-32.

Mengual X., Ståhls G., Rojo S. 2015. Phylogenetic relationships and taxonomic ranking of pipizine flower flies (Diptera: Syrphidae) with implications for the evolution of aphidophagy. *Cladistics* 31(2015): 491-508.

Micó E. 2018. Saproxylic Insects in Tree Hollows (pp. 693-727). *In:* Ulyshen M. (eds), Saproxylic Insects. Zoological Monographs, vol 1. *Springer, Cham.* 904 pp. DOI: 10.1007/978-3-319-75937-1_21

Miličić M., Janković M., Tot T., Nedeljković Z., Popov S., Ivošević B., Radenković S., Vujić A. 2018. New findings of hoverfly fauna (Diptera: Syrphidae) of the western part of Serbia (Zlatibor and Raška districts). *Acta entomologica serbica* 23(2): 43-66.

Monteil C. 2010. A Species Selection Tool for the "Syrph the Net" database. *In*: Speight M.C.D., Castella E., Sarthou J.-P., Monteil, C. (eds), Syrph the Net on CD, Issue 7. *The database of European Syrphidae. Syrph the Net Publications, Dublin.*

Müller O.F. 1764. *Favna insectorvm Fridrichsdalina* ... xxiv + 96 pp. *Io. Frid. Gleditschii, Hafniae et Lipsiae [= Copenhagen and Leipzig].*

Nedeljković Z., Ačanski J., Vujić A., Obreht D., Đan M., Ståhls G., Radenković S. 2013. Taxonomy of *Chrysotoxum festivum* Linnaeus, 1758 (Diptera: Syrphidae) – an integrative approach. *Zoological Journal of the Linnean Society* 169: 84-102.

Nedeljković Z., Ricarte A., Šašić Zorić Lj., Đan M., Obreht Vidaković D., Vujić A. 2018. The genus *Xanthogramma* Schiner, 1861 (Diptera: Syrphidae) in southeastern Europe, with descriptions of two new species. *Canadian Entomologist* 150: 440-464.

Nielsen T. 1970. *Cheilosia sootryeni* n.sp. (Diptera, Syrphidae), a Norwegian Species Resembling Ch. Vernalis Fallén. *Norsk entomologisk Tidsskrift* 17: 115-118.

Osten-Sacken C.R. 1875. On the North American species of the genus *Syrphus* (in the narrowest sense). *Proceedings of the*

Boston Society of Natural History (1875-1876) 18: 135-153.

Panzer G.W.F. 1798. Favnae insectorvm germanicae initia oder Deutschlands Insecten. Heft 60. *H. Felsecker, Nürnberg* 6, 24 pp.

Peck L.V. 1988. Syrphidae (pp. 11-363). *In:* Soos A., Papp, L. (eds), Catalogue of Palaearctic Diptera. *Akadémiai Kiadó, Budapest*, 8: 363 pp.

Poda von Neuhaus N. 1761. *Insecta musei Graecensis, quae in ordines, genera et species juxta Systema Naturae Caroli Linnaei digessit. Widmanstadii, Graecii [=Graz]* 127 + [xii] pp., 2 pls.

Popov S., Miličić M., Diti I., Oskar M., Sommaggio D., Markov Z., Vujić A. 2017. Phytophagous hoverflies (Diptera: Syrphidae) as indicators of changing landscapes. *Community Ecology* 18(3): 287-294.

Pujade-Villar J. 2011. Aproximació a la història de l'estudi entomològic-faunístic als Països Catalans i algunes reflexions sobre el present i el futur de la ciència dels hexàpodes. *Butlletí de la Institució Catalana d'Història Natural* 76: 5-46.

Rafinesque C.S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. *[Privately printed], Palermo*. 224 pp.

Ricarte A., Marcos-García M.A. 2008. Los sírfidos (Diptera: Syrphidae) del Parque Nacional de Cabañeros (España): una herramienta para la gestión. *Boletín de la Asociación Española de Entomología* 32(1-2): 19-32.

Ricarte A., Marcos-García M.A. 2017. A checklist of the Syrphidae (Diptera) of Spain, Andorra and Gibraltar. *Zootaxa* 4216(5): 401-440.
DOI: 10.11646/zootaxa.4216.5.1

Ricarte A., Nedeljković Z. 2020. *Triglyphus primus* Loew, 1840 (Diptera, Syrphidae), new to Spain. *Boletín de la Asociación Española de Entomología* 44(3-4): 567-570.

Ricarte A., Nedeljković Z., Quinto J., Marcos-García M.A. 2010. The Genus *Ferdinandea* Rondani, 1844 (Diptera, Syrphidae) in the Iberian Peninsula: First Records and New Breeding Sites. *Journal of the Entomological Research Society* 12(3): 57-69.

Rojo S., Gilbert F., Marcos-García M.A., Nieto J.M., Mier M.P. 2003. A world review of predatory hoverflies (Diptera, Syrphidae: Syrphinae) and their prey. *Alicante: Centro Iberoamericano de la Biodiversidad*, 319 pp.

Rondani C. 1844. Species Italicae Generis Callicerae ex insectis Dipteris, distinctae et descriptae; Fragmentum octavum ad inserviendum Dipterologiae Italicae. *Annales de la Société entomologique de France* (2) 2: 61-68.

Rondani C. 1845. *Species Italicae generis Chrysotoxi insectis Dipteris, observatae et distinctae. Fragmentum decimumad inserviendum dipterologiae Italicae. Annales de la Société entomologique de France* (2) 3: 193-203.

Rondani C. 1857. *Dipterologiae italicae prodromus.* Vol: II. *Species italicae ordinis dipterorum in genera characteribus defi nita, ordinatim collectae, methodo analitica distinctae, et novis vel minus cognitis descriptis. Pars prima. Oestridae: Syrpfhidae: Conopidae. A. Stocchi,* Parmae [= Parma], 264 pp.

Rondani C. 1865. *Diptera Italica non vel minus cognita descripta vel annotata observationibus nonnullis additis.* Fasc. I. Oestridae-Syrphidae-Conopidae; Fasc. II. Muscidae. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 8: 127-146 [May 1865]; 193-231 [May 1865].

Rotheray G.E. 1993. Colour guide to hoverfly larvae (Diptera, Syrphidae) in Britain and Europe. *Dipterists Digest* 9: 1-156.

Sacasas-i-Lluís J. 2009. El Ripollès. Territori i Paisatge. *Publicacions de l'Abadia de Montserrat: Barcelona*, 94 pp.

Sack P. 1928-1932. Die Fliegen der Palaerktischen Region, 31. Syrphidae. *Stuttgart (Schweizerbart)*, 451 pp.

Sánchez-Heredia E.M., Aniorte N., Ricarte A., Marcos-García M.A. 2017. Diversidad de sírfidos (Diptera: Syrphidae) de la Estación Biológica de Torretes (Alicante, España). *Cuadernos de Biodiversidad* 52: 38-45.

Schummel T.E. 1843. Verzeichniss und Beschreibung der bis jetzt in Schlesien gefangenen Zweiflügler der Syrphen Familie. Übersicht der Arbeiten und Veränderungen der Schlesischen Gesellschaft für vaterländische Kultur *im Jahre* 1842: 163-170.

Scopoli J.A. 1763. *Entomologia carniolica* ... I. T. Trattner, Vindobonae [=Vienna]. [36] + 420 + [1] pp.

Séguy E. 1961. Diptères Syrphides de l'Europe occidentale. *Mémoires du Muséum National d'Histoire Naturelle. Nouvelle Série, A, Zoologie* 23: 248 pp.

Shatalkin A.I. 1975. Taxonomic analysis of the family Syrphidae (Diptera). II. *Entomologicheskoe Obozrenie* 54: 899-909.

Sommaggio D. 2001. The species of the genus *Chrysotoxum* Meigen, 1822 (Diptera, Syrphidae) described by Giglio Tos. *Bollettino Museo Regionale di Scienze Naturali Torino* 18(1): 115-126.

Sommaggio D., Corazza C. 2006. Contributo alla conoscenza dei Sirfidi (Diptera Syrphidae) della città di Ferrara. *Quaderni della Stazione di Ecologia, Museo Civico di Storia Naturale, cita di Ferrara* 16: 5-20.

Speight M.C.D. 2020. Species accounts of European Syrphidae, *2020. Syrph the Net, the database of European Syrphidae (Diptera). Syrph the Net publications, Dublin* 104: 1-314.

Speight M.C.D., Castella E. 2001. An approach to interpretation of lists of insects using digitised biological information about the species. *Journal of Insect Conservation* 5: 131-139.

Speight M.C.D., Sarthou J.-P. 2017. StN keys for the identification of the European species of various genera of Syrphidae 2017/Clés StN pour la détermination des espèces européennes de plusieurs genres de Syrphidae 2017. *Syrph the Net, the database of European Syrphidae (Diptera). Syrph the Net publications, Dublin* Vol. 99, 139 pp.

Speight M.C.D., Sommaggio D. 2010. On the presence in Switzerland of *Microdon myrmicae* Schönrogge et al., 2002, *Xanthogramma dives* (Rondani, 1857) and *X. stackelbergi* Violovitsh, 1975 (Diptera: Syrphidae). *Entomo Helvetica* 3: 139-145.

Speight M.C.D., Castella E., Sarthou J.-P. 2020. StN 2020. *In:* Speight M.C.D., Castella E., Sarthou J.-P., Vanappelghem C. (eds), Syrph the Net on CD, Issue 12. *Syrph the Net Publications, Dublin.*

Ståhls G., Vujić A., Milankov V. 2008. *Cheilosia vernalis* (Diptera, Syrphidae) complex: molecular and morphological variability. *Annales Zoologici Fennici* 45: 149-159.

Thompson F.C., Torp E. 1986. Synopsis of the European species of *Sphegina* Meigen (Diptera: Syrphidae). *Fauna Entomologica scandinavica* 17: 235-268.

van Doesburg P.H. 1951. Syrphidae de Banyuls et environs. 10me communication sur les diptères syrphides. *Vie et milieu* 2(4): 481-487.

van Eck A. 2010. Poorly recorded Syrphidae (Diptera) from

Spain including species new to its fauna. *Boletín de la Sociedad Entomológica Aragonesa*, 46: 299-300.

van Steenis 2000. The West-Palaearctic species of *Spilomyia* Meigen (Diptera: Syrphidae). *Bulletin de la Société Entomologique Suisse* 73: 143-168.

van Steenis J., Lucas J.A.W. 2011. Revision of the West-Palaearctic species of *Pipizella* Rondani, 1856 (Diptera, Syrphidae). *Dipterists Digest* 18: 127-180.

van Steenis J., Ricarte A., Vujić A., Birtele D., Speight M.C.D. 2016. Revision of the West-Palaearctic species of the tribe Cerioidini (Diptera, Syrphidae). *Zootaxa* 4196 (2): 151-209.

van Steenis J., van Zuijen M.P., Ricarte A., Marcos-García M.A., Doczkal D., Ssymank A., Mengual X. 2020. First records of *Chrysotoxum volaticum* Séguy, 1961 from Europe and *Platycheirus marokkanus* Kassebeer, 1998 from Spain (Diptera: Syrphidae) together with additional records of Spanish *Chrysotoxum* Meigen, 1803. *Bonn zoological Bulletin* 69(1): 141-155.

van Veen M. 2010. Hoverflies of Northwest Europe: identification keys to the Syrphidae. *KNNV Publishing, Utrecht, Netherlands,* 247 pp.

Vázquez V.M., Fernández-Prieto J.A. 2002. El bosque Atlántico (pp. 48-69). *In:* Reyero J.M. (ed), La Naturaleza de España. *Ministerio de Medio Ambiente, Madrid*, 381 pp.

Verlinden L. 1999. *Cheilosia hypena* Becker, 1894 (Diptera, Syrphidae) - description of the male, re-description of the female and its separation from *Cheilosia frontalis* Loew, 1857. *Volucella* 4(1/2): 85-92.

Verrall G.H. 1873. Additions and correction to the list of British Syrphidae. *Entomologist's Monthly Magazine* 9: 251-256.

Violovitsh N.A. 1974. A review of the Palaearctic species of the genus *Chrysotoxum* Mg. (Diptera, Syrphidae). *Entomologocskoc obozrenie (Entomological Review)* 53: 196-217.

Vujić A. 1992. Taksonomski položaj i zoogeografska analiza roda *Cheilosia* Meigen, 1822 i srodnih rodova (Diptera: Syrphidae) na Balkanskom poluostrvu. *PhD thesis, University of Novi Sad, Serbia,* 260 pp.

Vujić A. 1996. Genus *Cheilosia* Meigen and related genera (Diptera: Syrphidae) on the Balkan Peninsula. *Monographs of Matica Srpska, Novi Sad*, 194 pp.

Vujić A. 1999. The tribe Chrysogasterini (Diptera: Syrphidae) in the Balkan Peninsula, with the description of three new cryptic species. *Studia dipterologica* 6(2): 405-423.

Vujić A., Nedeljković A., Hayat R., Demirözer O., Mengual X., Kazerani F. 2017. New data on the genus *Chrysotoxum* Meigen (Diptera: Syrphidae) from North-East Turkey, Armenia, Azerbaijan and Iran including descriptions of three new species. *Zoology in the Middle East* 63(3): 250-268.

Vujić A., Radenković S., Trifunov S., Nikolić T. 2013. Key for European species of the *Cheilosia proxima* group (Diptera, Syrphidae) with a description of a new species. *ZooKeys* 269: 33-50.

Vujić A., Ståhls G., Ačanski J, Bartsch H., Bygebjerg R., Stefanović A. 2013. Systematics of Pipizini and taxonomy of European *Pipiza* Fallén: molecular and morphological evidence (Diptera, Syrphidae). *Zoologica Scripta* 42(3): 288-305.

Vujić A., Šimić S. 1995-1998. Genus *Eumerus* Meigen 1822 (Diptera: Syrphidae) in area of former Jugoslavia. *Glasnik Prirodnjackog Muzeja u Beogradu* B 49-50: 173-190.

Wiedemann C.R.W. 1818. Neue Insecten vom Vorgebirge der guten Hoffnung. *Zoologisches Magazin* 1(2): 40-48.

Zetterstedt J.W. 1838. *Dipterologis Scandinaviae.* Sect. 3: Diptera, pp. 477-868. *Insecta Lapponica, Lipsiae [= Leipzig],* vi + 1, 140 pp.

Zetterstedt J.W. 1842-1860. *Diptera Scandinaviae, Officina Lundbergiana, Lundae [= Lund.],* Vol. 1, [before 06.09.1842]; vol. 2, pp. 441-894 [02.05.1843]; vol. 3, pp. 895-1012 [20.03.1844], 1013-1280 [09.04.1845]; vol. 4, pp. 1281-1738 [11.06.1845]; vol. 5, pp. 1739-2162[03.09.1846]; vol. 6, pp. 2163-2580 [09.06.1847]; vol. 7, pp. 2581-2934 [13.09.1848]; vol. 8, pp. 2935-3366 [12.09.1849]; vol. 9, pp. 3367-3710 [1850]; vol. 10, pp. 3711-4090 [1851]; vol. 11, pp. 4091-4545[10.03.1852]; vol. 12, pp. xx + 4547-4942 [July 1855]; vol. 13, pp. xvi+ 4943-6190 [01.091859 preface]; vol. 14, pp. iv + 6191-6609 [12.12.1860], pp. iii-xvi+440.

APPENDIX

First faunistic data on the hoverflies from the eastern Pyrenees of Girona province (Spain) collected in July/August 2020. (*) indicates the first documented record of a species for a geographical unit, i.e. the species was known from a geographical unit but without further locality details and this is the first time that locality details are provided. *Triglyphus primus* is omitted from this list because its records were advanced in a different publication.

	Nested geographical units in ascending order			
New to:	**Girona**	**Catalonia**	**Spain**	**Iberian Pen.**
Chrysotoxum lessonae	■	■	■	■
*Xylota tarda**	■	■	■	■
*Cheilosia hypena**	■	■	■	
Ceriana conopsoides	■	■		
Cheilosia aerea	■	■		
Cheilosia barbata	■	■		
Cheilosia illustrata	■	■		
Cheilosia longula	■	■		
*Cheilosia proxima**	■	■		
Cheilosia vicina	■	■		
Chrysotoxum arcuatum	■	■		
Chrysotoxum elegans	■	■		
Eristalis similis	■	■		
Eumerus grandis	■	■		
Eumerus ornatus	■	■		
Helophilus pendulus	■	■		
Melangyna umbellatarum	■	■		
Meligramma cincta	■	■		
Meliscaeva cinctella	■	■		
Sericomyia bombiforme	■	■		
Scaeva dignota	■	■		
*Sphegina elegans**	■	■		
Cheilosia latifrons	■			
Cheilosia variabilis	■			

	Nested geographical units in ascending order				
	New to:	**Girona**	**Catalonia**	**Spain**	**Iberian Pen.**
Chrysotoxum festivum					
Eristalinus taeniops					
Eristalis interrupta					
Eristalis jugorum					
Eristalis pertinax					
Ferdinandea cuprea					
Lapposyrphus lapponicus					
Melangyna compositarum					
Meliscaeva auricollis					
Orthonevra nobilis					
Parasyrphus vittiger					
Pipiza festiva					
Pipiza noctiluca					
Pipizella viduata					
Platycheirus albimanus					
Spilomyia manicata					
Syrphus torvus					
Volucella pellucens					
Xanthandrus comtus					
Xylota segnis					
Xylota sylvarum					

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Species-group organization of the Pan-American *Dissomphalus* (Hymenoptera, Bethylidae)

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Abstract: *Dissomphalus* is a cosmopolitan genus with 424 described species. Here, all 287 Pan-American species of *Dissomphalus* are analyzed in order to be allocated to species groups under an alpha taxonomic approach. Thirty-four species groups composed of species with known males were initially considered. The following six species-groups are newly proposed: *chiapanus*, *confusus*, *cornutus*, *fungosus*, *lamellatus* and *napo*. The following eleven species groups are fused into four: *dissomphaloides* with *amplus*, *altivolans* with *apertus*, *xanthopus* with *microstictus*, *kansanus* with *secretus*, *basidentatus* and *stellatus* with *vallensis*, and *strabus* with *tuberculatus*. Forty-seven *incertae sedis* species are grouped and 29 are newly grouped. A total of 35 species groups are now recognized and all of the 11 species known exclusively by females remain unallocated to groups. A pictorial key to the species groups is first proposed.

Keywords: Alpha taxonomy - Chrysidoidea - Nearctic - Neotropical - Pristocerinae - synopsis.

INTRODUCTION

Dissomphalus Ashmead (Fig. 1) is hitherto the largest genus of Bethylidae with 442 valid species worldwide (Azevedo *et al.,* 2018b; Colombo *et al.,* 2018), of which 287 occur in the New Word. Nine species are recorded from the Nearctic region, and five of them are restricted to this regions, three range to Central America, and only *D. krombeini* Azevedo reaches South America (Azevedo, 2003). All the others 278 are distributed throughout the Neotropical region.

Evans (1955 [1954]) was the first to organize *Dissomphalus* into species groups, when he proposed the *xanthopus* and *apertus* species groups for the eight North American species valid at that time. Soon after, Evans (1962) added the *kansanus* species group and included species from Mexico and the Caribbean islands. However, some species were left unallocated.

Alencar & Azevedo (2006, 2008), Azevedo (1999a, 2000, 2001, 2003), Colombo & Azevedo (2016) and Redighieri & Azevedo (2006) organized the Neotropical *Dissomphalus* in 32 groups. During these years, hundreds of new species were described, many of them in studies focused on a particular geographical area, such as Azevedo (1999b), Brito & Azevedo (2017), Colombo & Azevedo (2016), Colombo *et al.* (2018) and Redighieri & Azevedo (2004, 2006). However, many species published in these studies were not allocated in any species group.

Today there are four main problems with the alpha taxonomy of Pan-American *Dissomphalus* related to the species-group organization. First, the organization by Evans was focused mostly on Nearctic species at a time when the genus had few valid species, and Azevedo and collaborators were focused mostly on Neotropical species. Both systems were not fully congruent. Second, there are about 50 species not allocated in any species group. Third, there are several fragmented keys for species group or at the species level covering restricted geographical areas. Thus, identifying any species of Pan-American *Dissomphalus* is a tough task because no key encompassing all species groups or species is available. Fourth, Evans's and Azevedo's group organizations were based on characters of the second metasomal tergal process, a structure of male metasoma, and on male genitalia, but mostly on the former. Thus, species known exclusively by females were never arranged in groups.

Given this scenario, the objective of this contribution is to solve the three first problems aforementioned by proposing a single species-group organization embracing all Pan-American species of *Dissomphalus* known from males.

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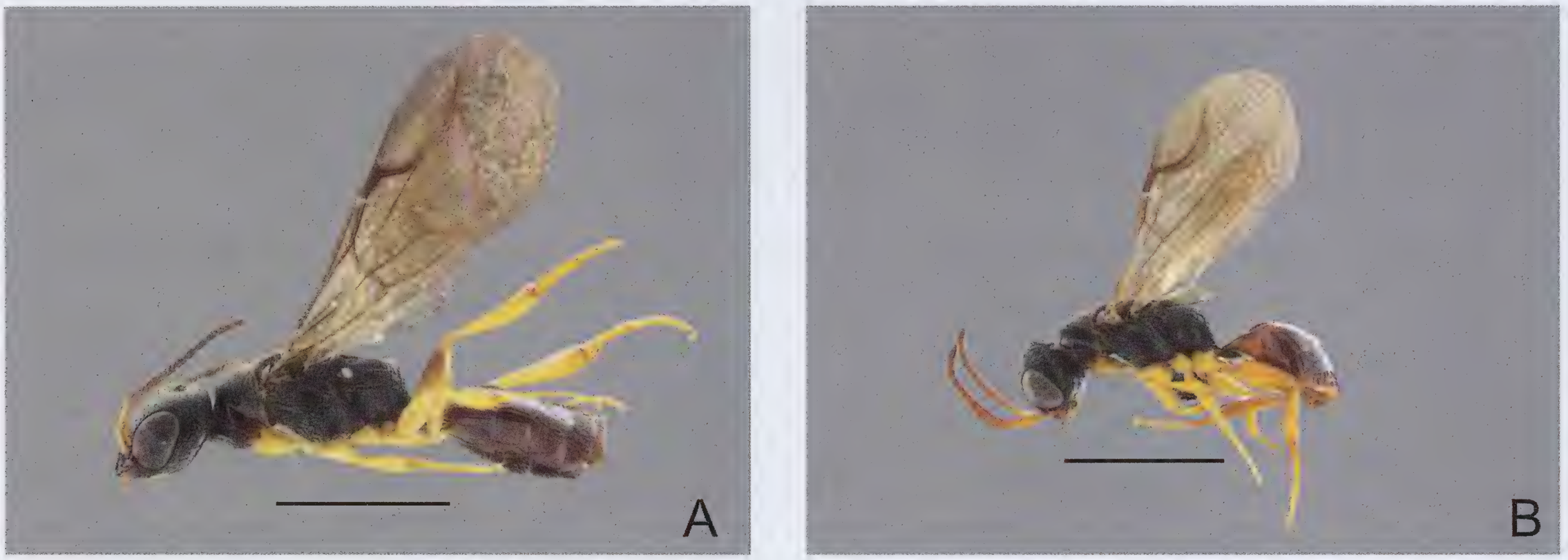


Fig. 1. Habitus of *Dissomphalus*. (A) Species group *bicavatus*. (B) Species group *conicus*. Scale bars 2 mm.

MATERIALS AND METHODS

This contribution is fully based on the original descriptions, further information and redescriptions of all species recorded from the Pan-Americas, their type series and any other voucher found in Alencar & Azevedo (2006, 2008), Ashmead (1893, 1894), Azevedo (1999a, b, c, 2000, 2001, 2003), Azevedo *et al.* (2016, 2018a, b), Brito & Azevedo (2017), Bruch (1916), Colombo & Azevedo (2016) Colombo *et al.* (2018), Evans (1955 [1954], 1962, 1963, 1964, 1966, 1969, 1978, 1979), Kieffer (1904, 1906 [1905], 1908, 1910a, b, 1911, 1914a, b), Ogloblin (1930), Redighieri & Azevedo (2004, 2006), Snelling (1996), Vargas & Terayama (2002), Wasmann (1899), Westwood (1839).

The dichotomous keys were drawn up by juxtaposition to identify the species-group, according to their most important characters. Most of the couplets are new, but those of species-groups with median tergal processes are mostly based on Azevedo (1999a). The main characters of each couplet are illustrated. The hand drawings are digitally prepared and represent fictitious specimens. Most of these illustrations are related to tergal processes on the second metasomal segment, which can have a wide range of structures.

I adopted a convention of three different structures in the line drawings. Depressions are a lowering of the surface with a smooth edge, drawn with dashed lines in all illustrations, for instance figure A at couplet 5 in the key. On the other hand, pits are holes on the surface with a sharp edge, clearly outlined, they are drawn with regular lines, for instance figure B at couplet 5 in the key. If the pit is very wide, I used the term concavity, for instance figure A at couplet 34 in the key.

The habitus of Figure 1 was photographed with a Leica Z16 APO stereomicroscope coupled to a Leica DFC 2 video camera with Leica Application Suite V3.6.0 by Leica Microsystems (Switzerland). The image stacks were combined with Helicon Focus (HeliconSoft) and posteriorly edited with Gimp 2.10 software.

The tubercles of the tergal processes are nodular protuberances on the surface of metasomal segment II. They have three orientations. When the tubercles are directed anterad, they are drawn turned forward, for instance figure A in couplet 21 in the key. When the tubercles are directed mesad, they are drawn toward median plane of the metasoma, for instance figure B at couplet 3 in the key. When the tubercles are directed dorsad, they are drawn directed posterad, otherwise the setae would appear in the illustrations as dots rather than filaments, for instance figure A at couplet 3 in the key.

The scope of this contribution is focused on species-group rank other than species level. Thus, the section with check lists of each species-group is not intended to be a catalog. So, only a list of all valid species is presented, without nomenclatural heading. The terms applied to structures follow Lanes *et al.* (2020).

RESULTS

I recognize 287 species of *Dissomphalus* occurring in the New World, organized in 35 species groups, six of them newly proposed. Eleven species known only from female specimens were not grouped.

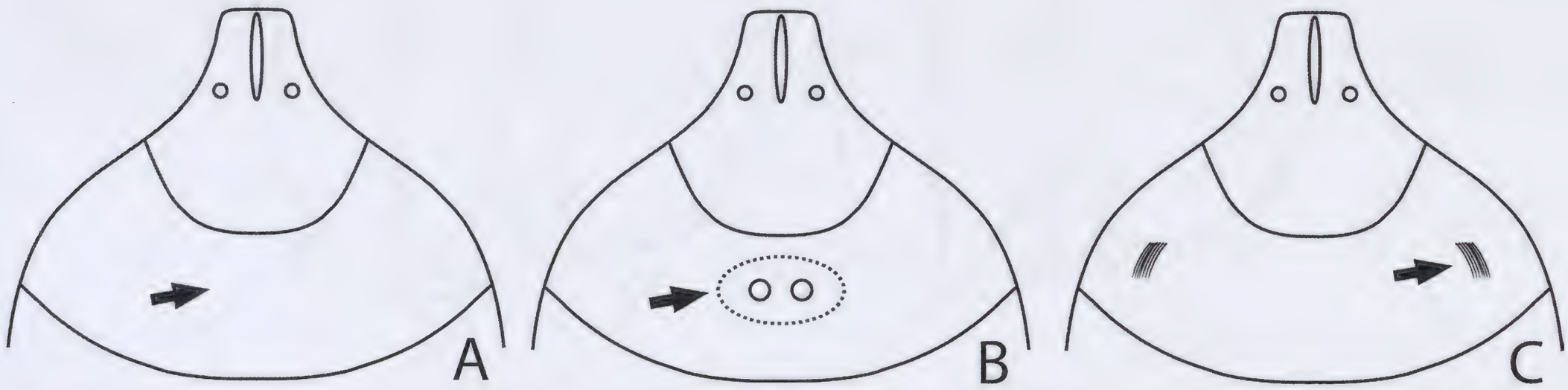
Key to species-groups of Pan-American *Dissomphalus* (♂)

Shortcuts to major groupings

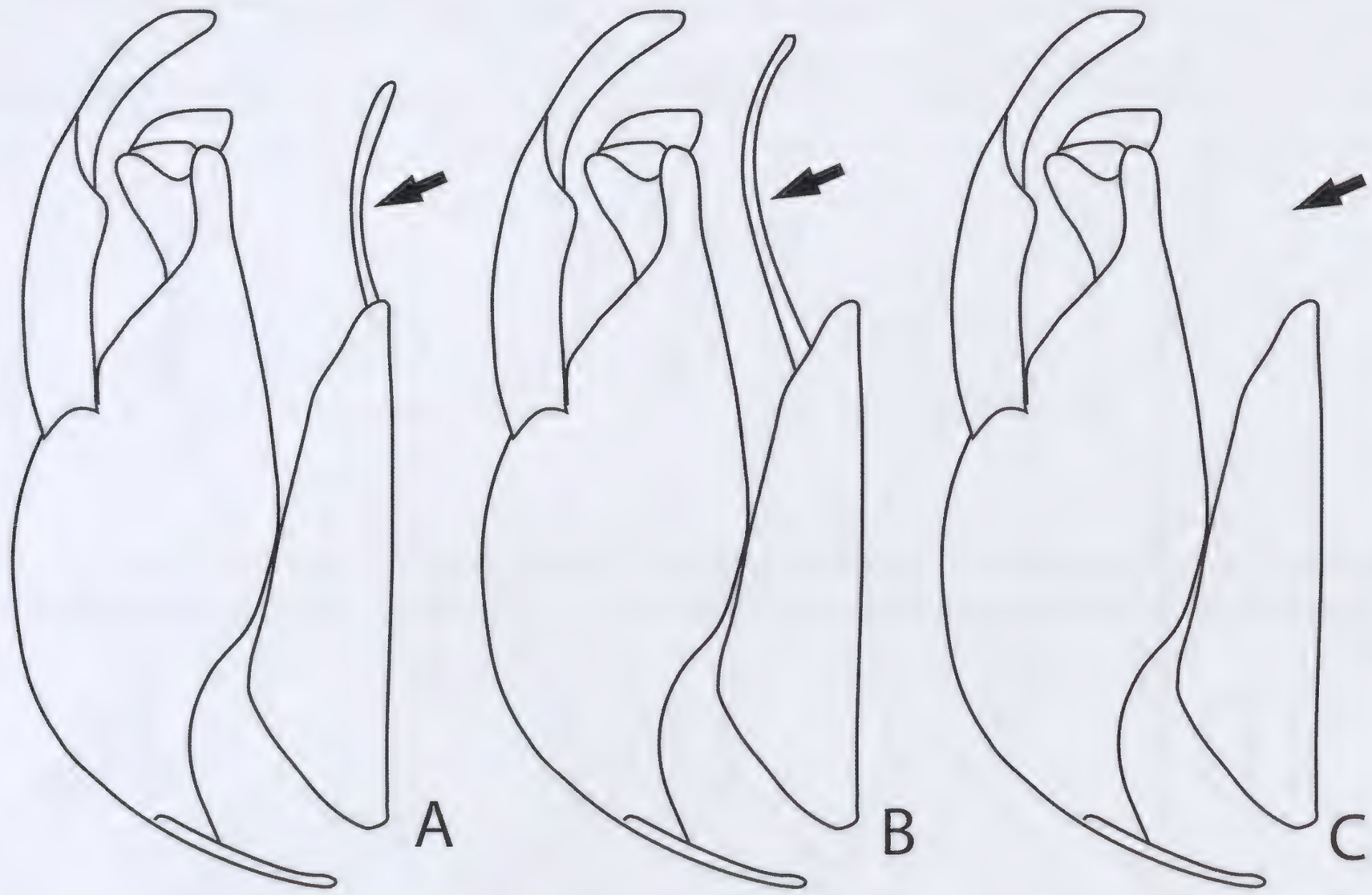
Tergal process absent 2
Tergal process present 5
Median tergal process 6
Lateral tergal process 16
Tergal process without tubercles 19
Tergal process with pair of pits 18
Tergal process with pair of tufts of setae, without any pit 20
Tergal process with pair of tubercles 28

Key to groups

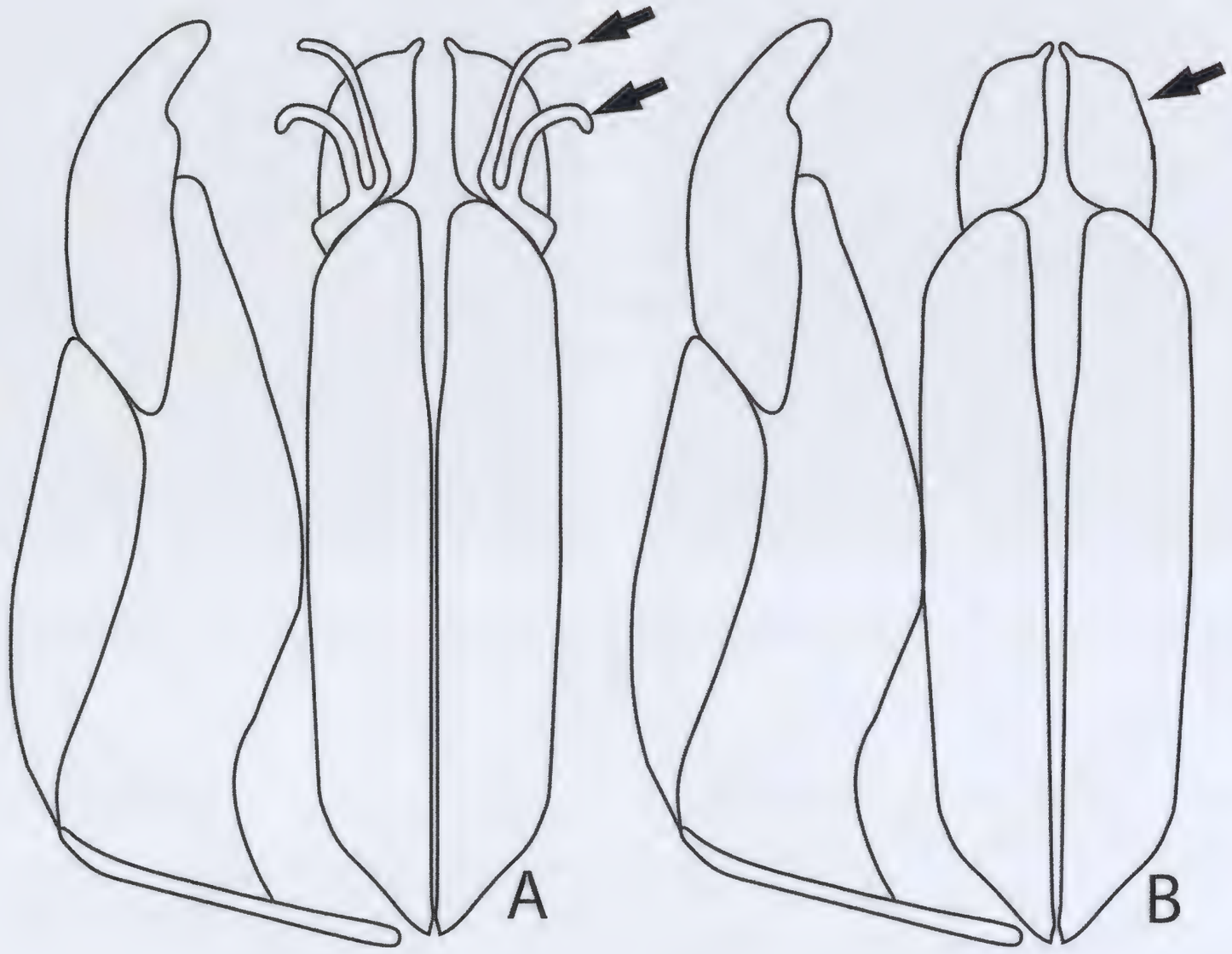
1. Tergal process absent (A) 2
– Tergal process present (B, C) 5



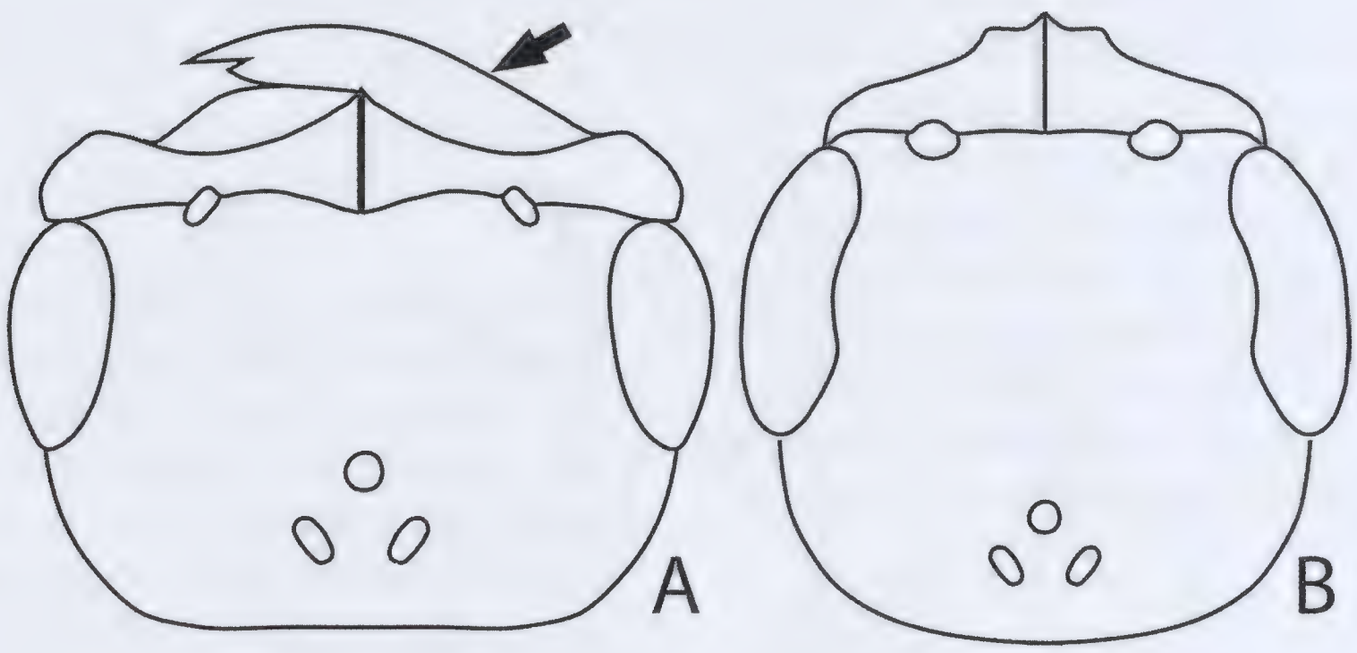
2. Apex of aedeagal ventral ramus with apical (A) or subapical (B) filament ..... *microstictus* (E.8)
– Apex of aedeagal ventral ramus without such filament (C) 3



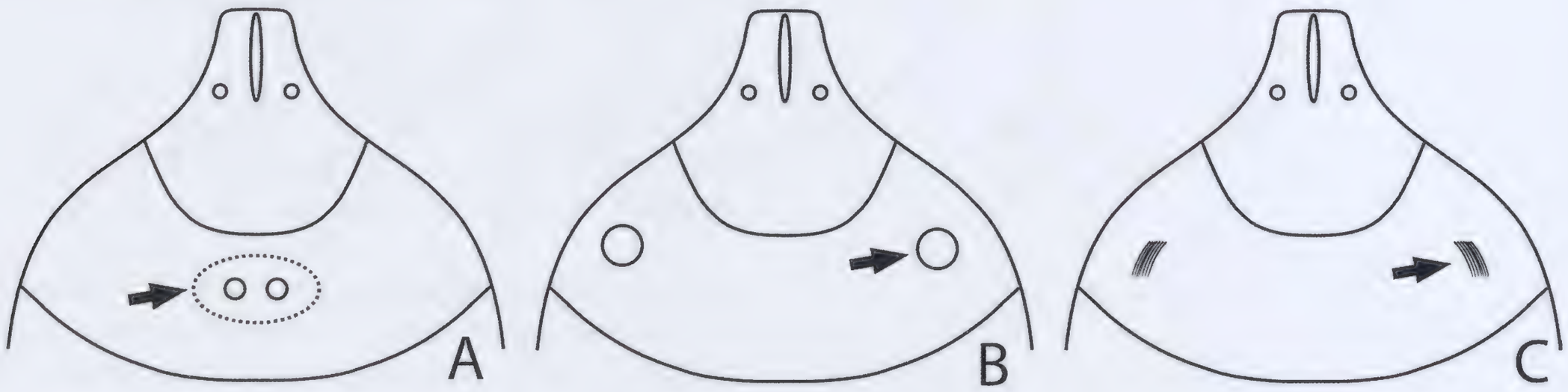
3. Aedeagal dorsal body with two pairs of flagella (A)..... *incomptus* (E.6)
– Aedeagal dorsal body without flagella (B).....4



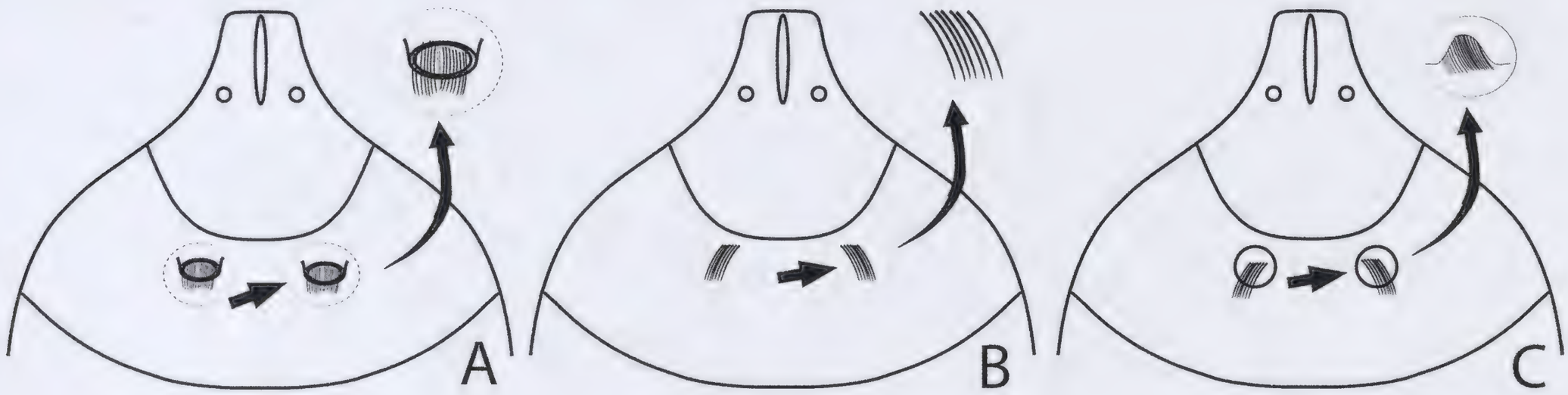
4. Mandibles unusually long, at least ~0.75 × as long as distance between their bases; head unusually wide, head much wider than long (A)..... *laticephalus* (E.7)
– Mandibles overlapping just a little bit when closed; head about as wide as long (B)..... *amplus* (A.1)



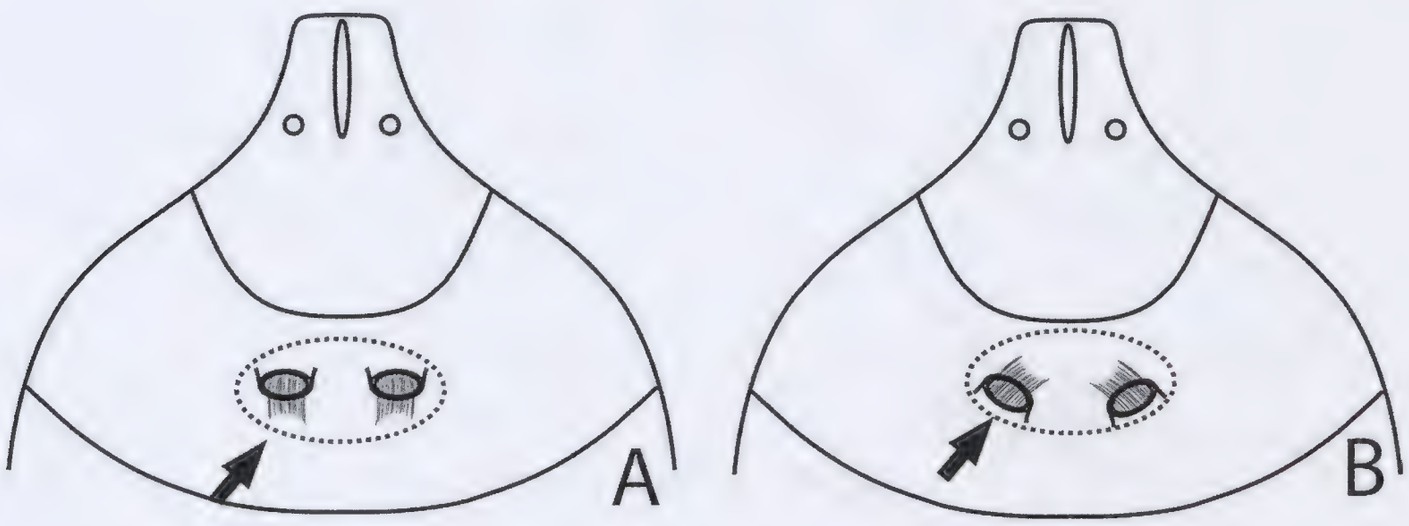
5. Tergal processes close to each other, located at middle of median third of tergal width (A).....6
– Tergal processes far from each other, located at lateral third of tergal width, or at most between lateral and median thirds (B, C).....16



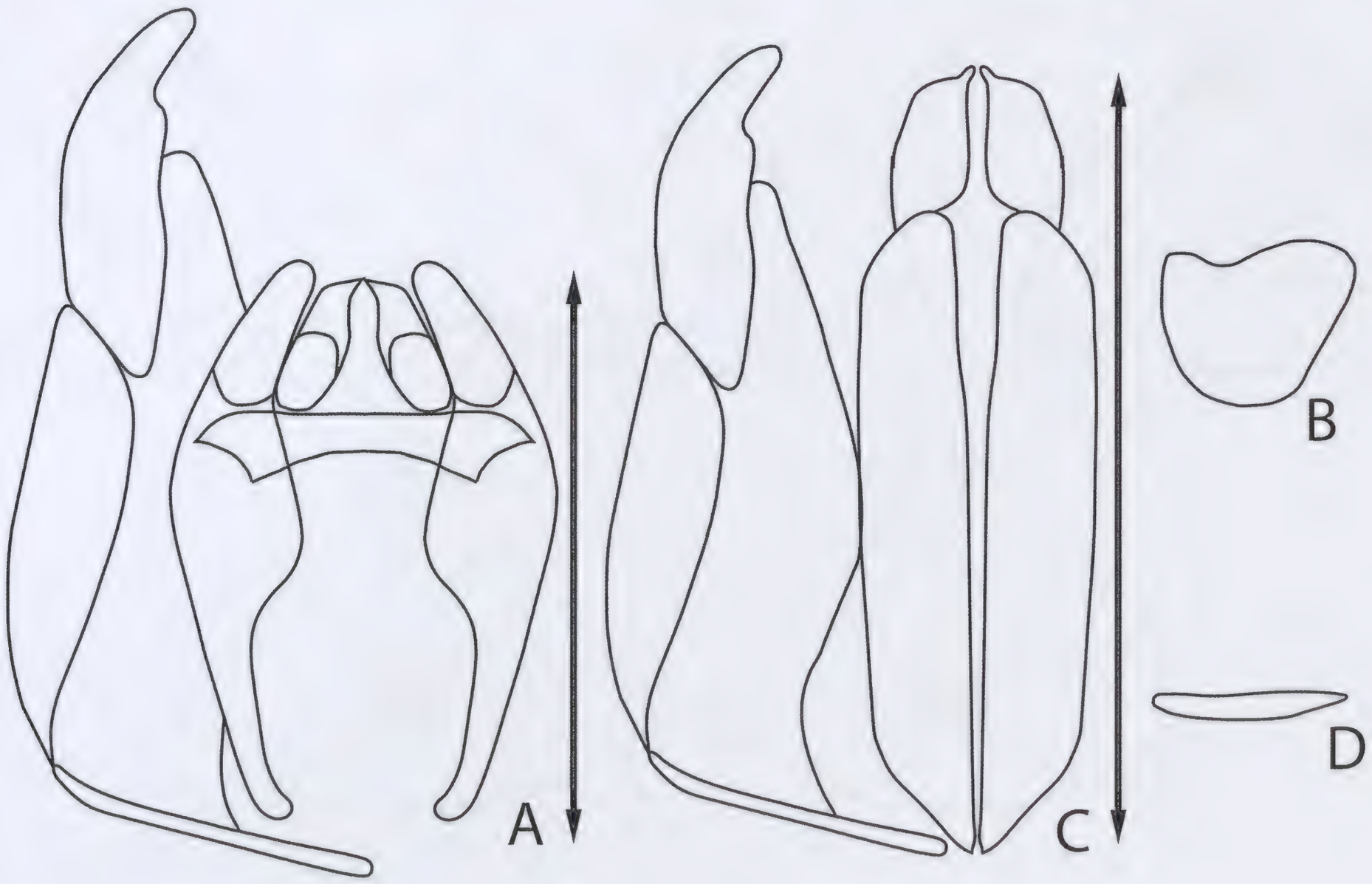
6. Tuft of setae of tergal processes raising from tubercles (A).....7
– Tuft of setae of tergal processes emerging from flat surface (B) or from pits (C), but never from tubercles 10



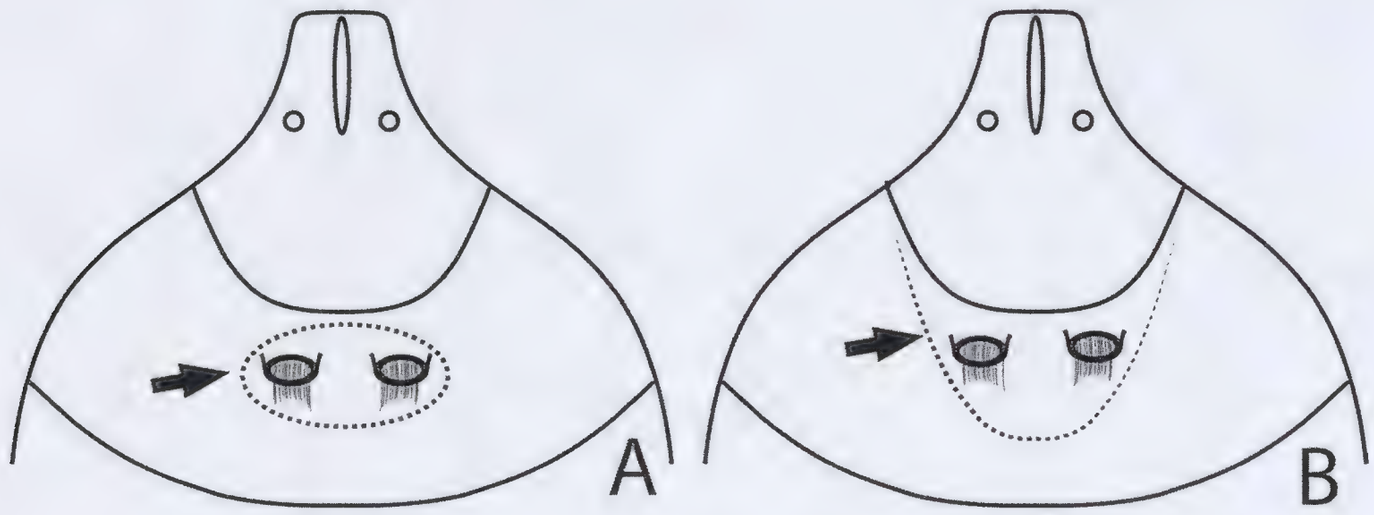
7. Tubercles of tergal processes located at middle of depression, tubercles in vertical position and running parallel (A).....8
– Tubercles of tergal processes located close to distal margin of depression, tubercles at least slightly directed towards each other (B)..... *vallensis* (B.11)



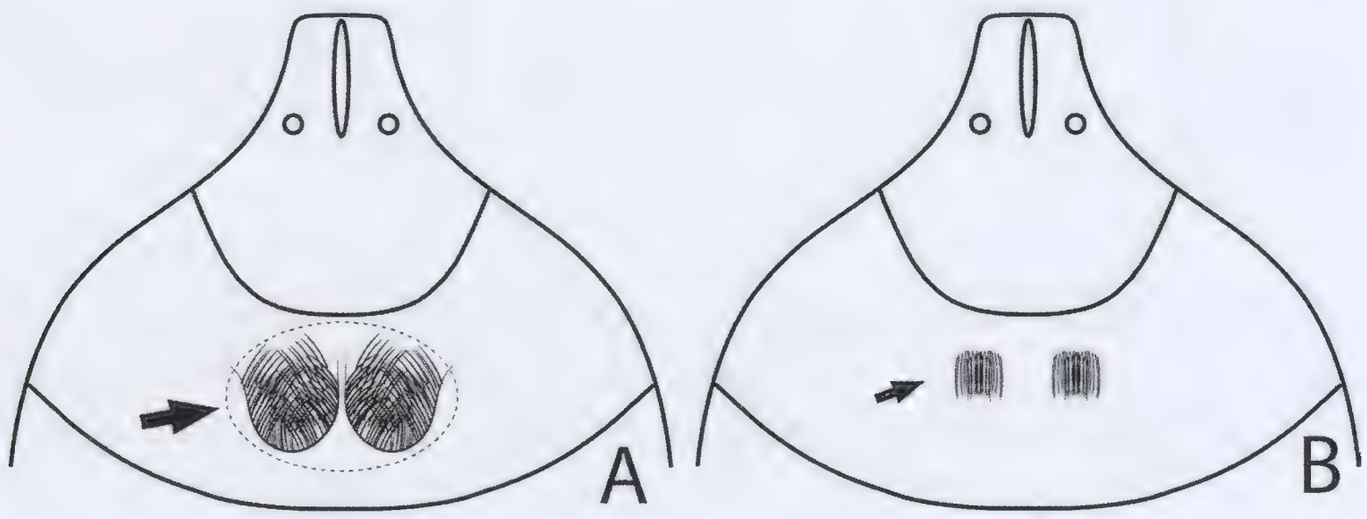
8. Aedeagal dorsal body very short, apex anterior to base of digitus (A); cross-section of aedeagal ventral ramus tubular (B).....*brasiliensis* (B.4)
– Aedeagal dorsal body long, apex posterior to base of digitus (C); cross-section of aedeagal ventral ramus flat (D) 9



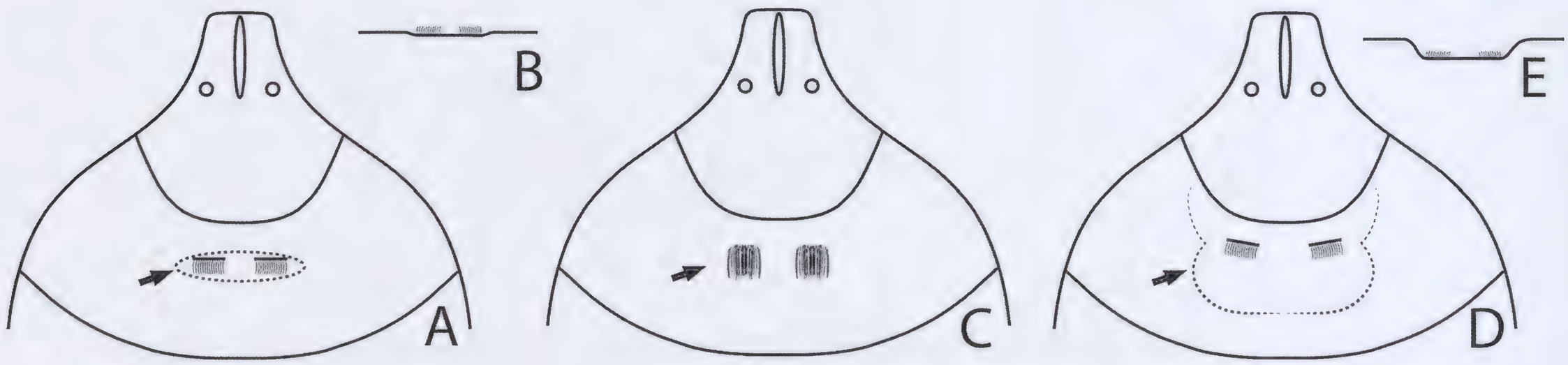
9. Depression of tergal processes elliptical, deep, not embracing posterior margin of metasomal tergite I (A)..... ..... *longiclypeus* (B.7)
– Depression of tergal processes half-moon-shaped, shallow, embracing posterior margin of metasomal tergite I (B)..... *rasissimus* (B.8)



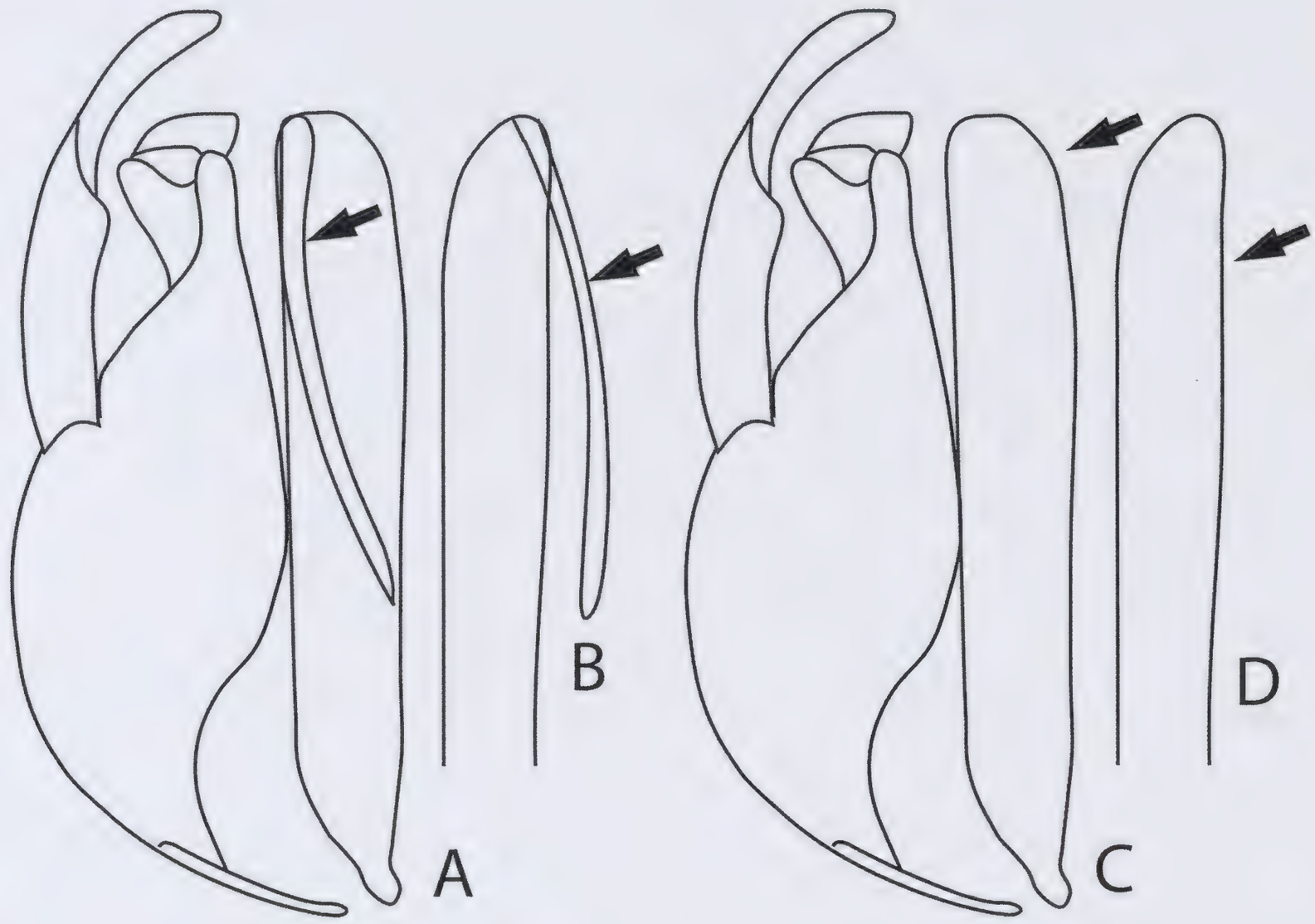
10. Tufts of setae of tergal processes emerging from pair of huge median pits (A).....*curvifoveatus* (B.5)
– Tufts of setae of tergal processes emerging directly from surface (B).....11



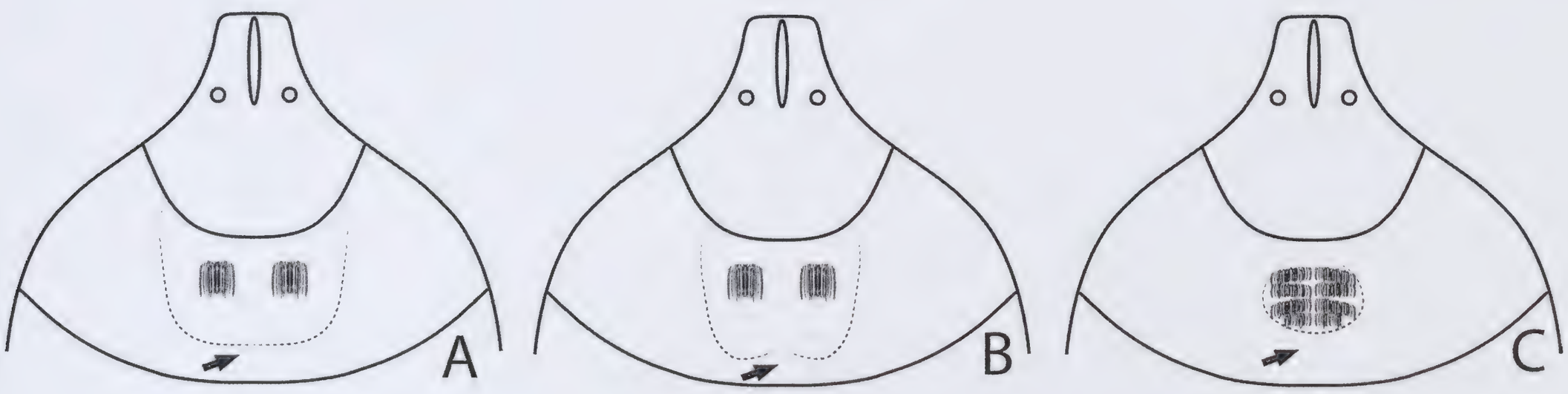
11. Tufts of setae of tergal processes pair linear and transverse (A) in shallow depression (B)..... *bisulcus* (B.3)
– Tufts of setae of tergal processes either non-linear (C), or linear in deep and broad depression (D, E).....12



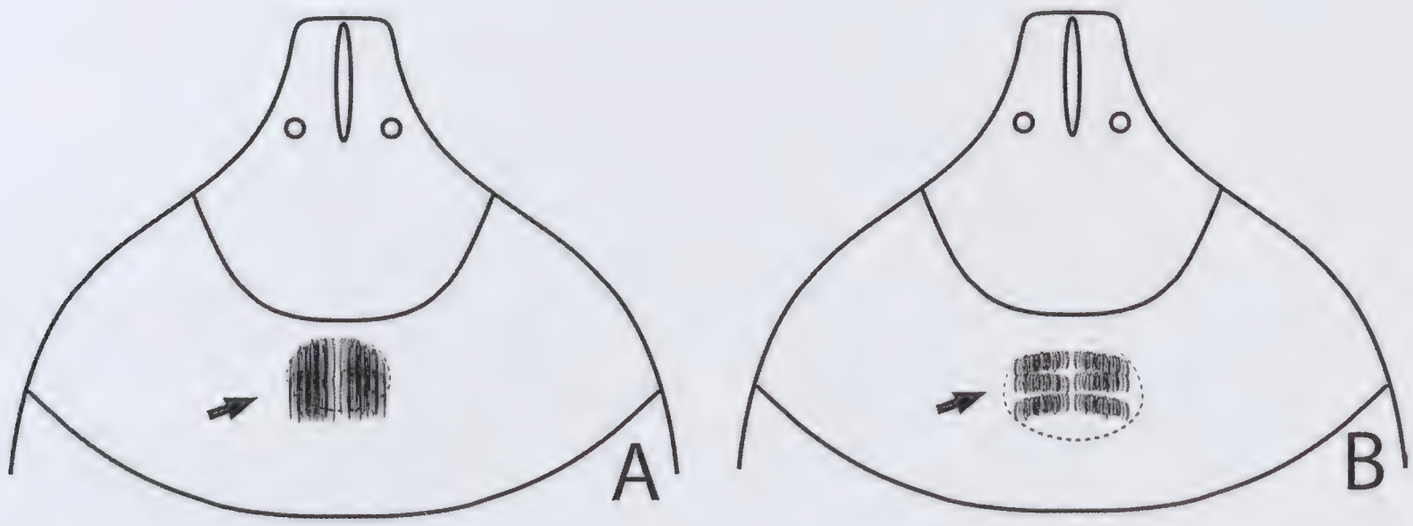
12. Aedeagal ventral ramus with filament strongly angled anterad and ventrad (A, ventral view; B, lateral view).....
.....*bifoveatus* (B.2)
– Aedeagal ventral ramus without such filament (C, ventral view; D, lateral view).....13



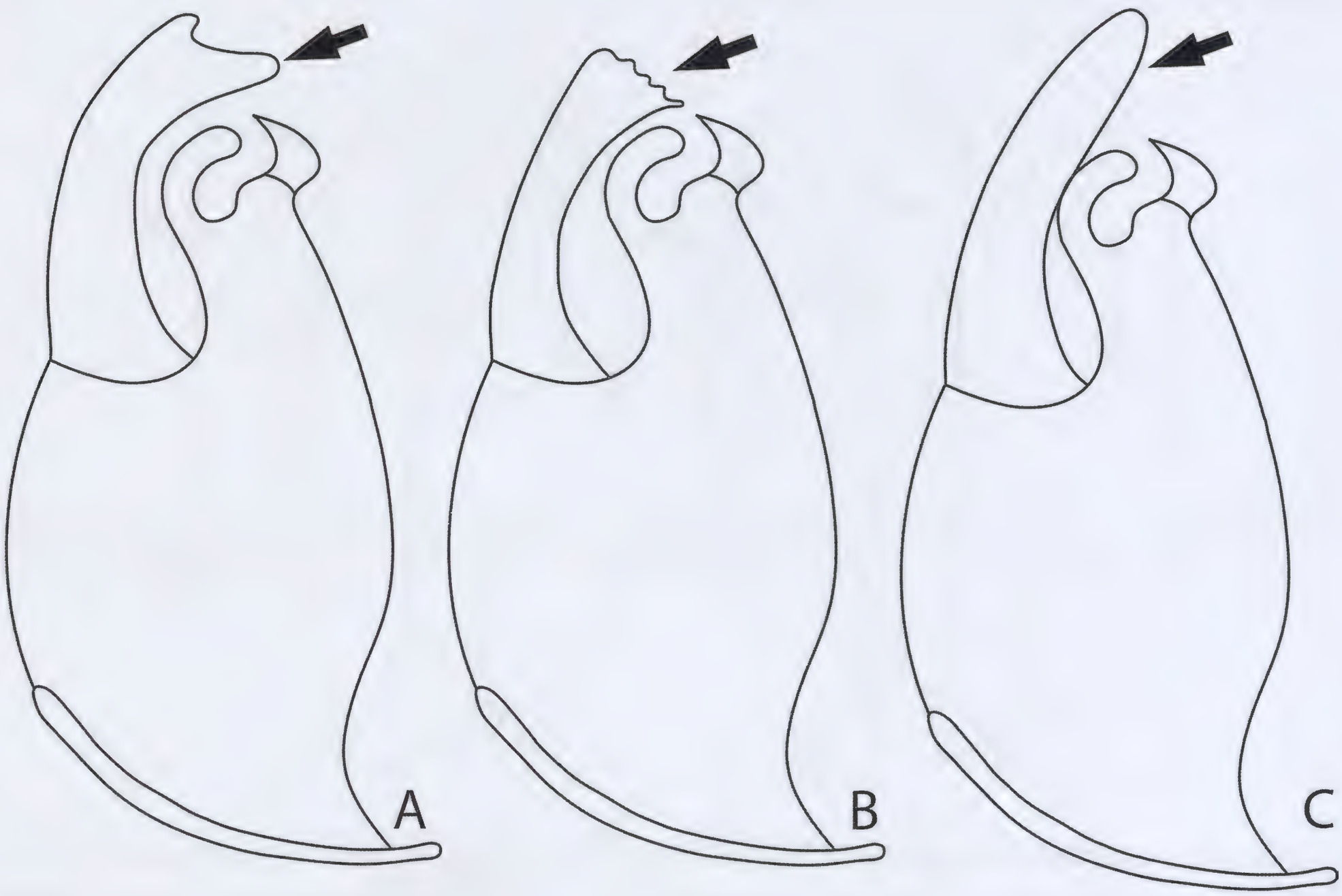
13. Depression of tergal processes half-moon-shaped or nearly so, with posterior margin complete (A) or partially faded (B).....*linearis* (B.6)
– Depression of tergal processes usually elliptical, subcircular or nearly so (C), but never half-moon-shaped.....14



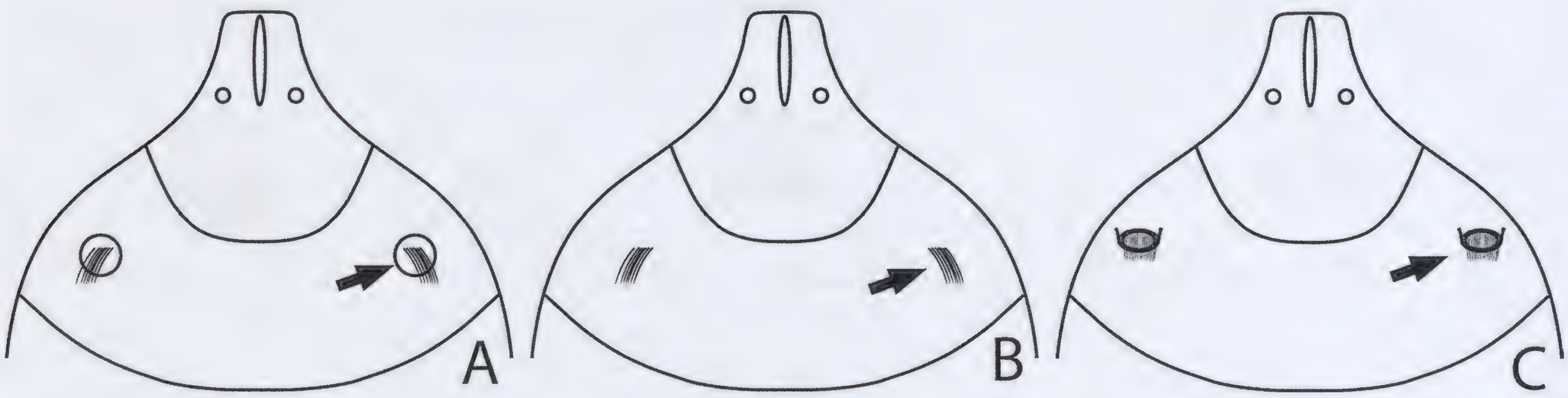
14. Tufts of tergal processes with setae as long as depression (A)..... *unitus* (B.10)
– Tufts of tergal processes with setae shorter than depression (B).....15



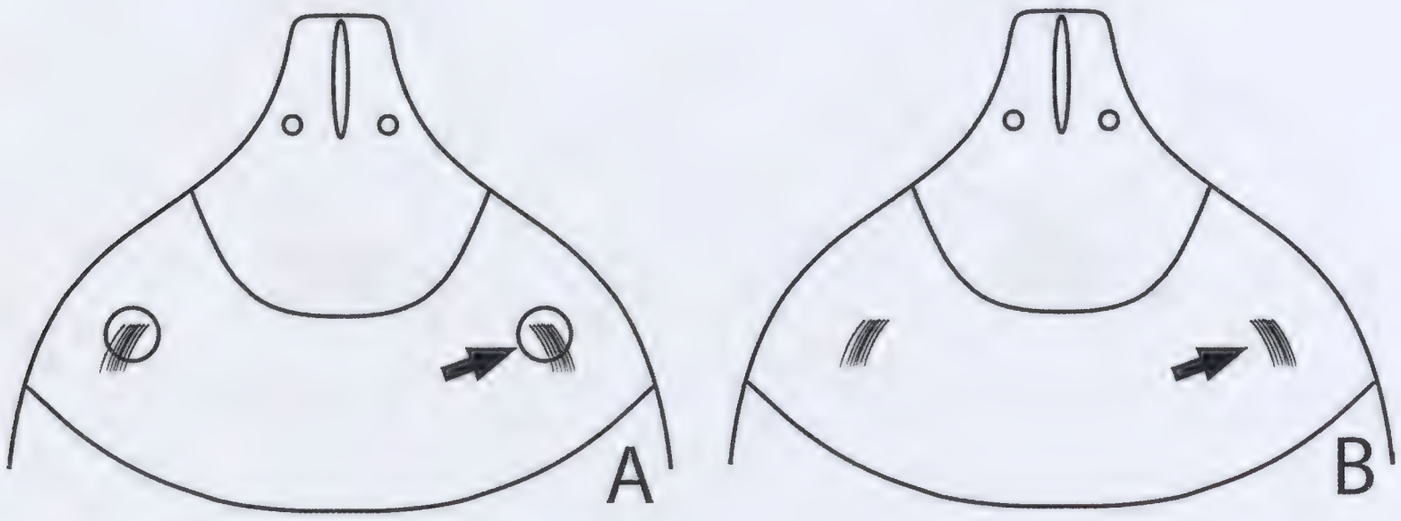
15. Corners of harpe apex angulate, margin between corners truncate, incurved (A) or dentate (B) ..... *ulceratus* (B.9)
– Apex of harpe smoothly tapering and rounded (C) ..... *apertus* (B.1)



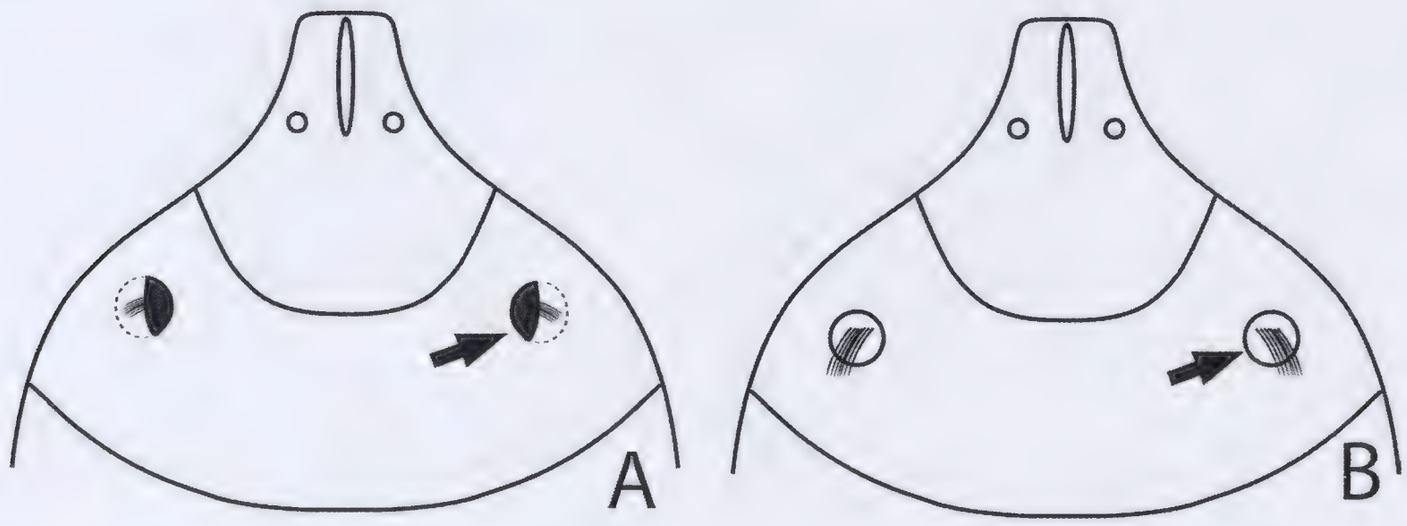
16. Tergal process with tuft of setae placed inside pit (A) or on surface (B), but never with tubercle 17
– Tergal process with tubercle (C).....28



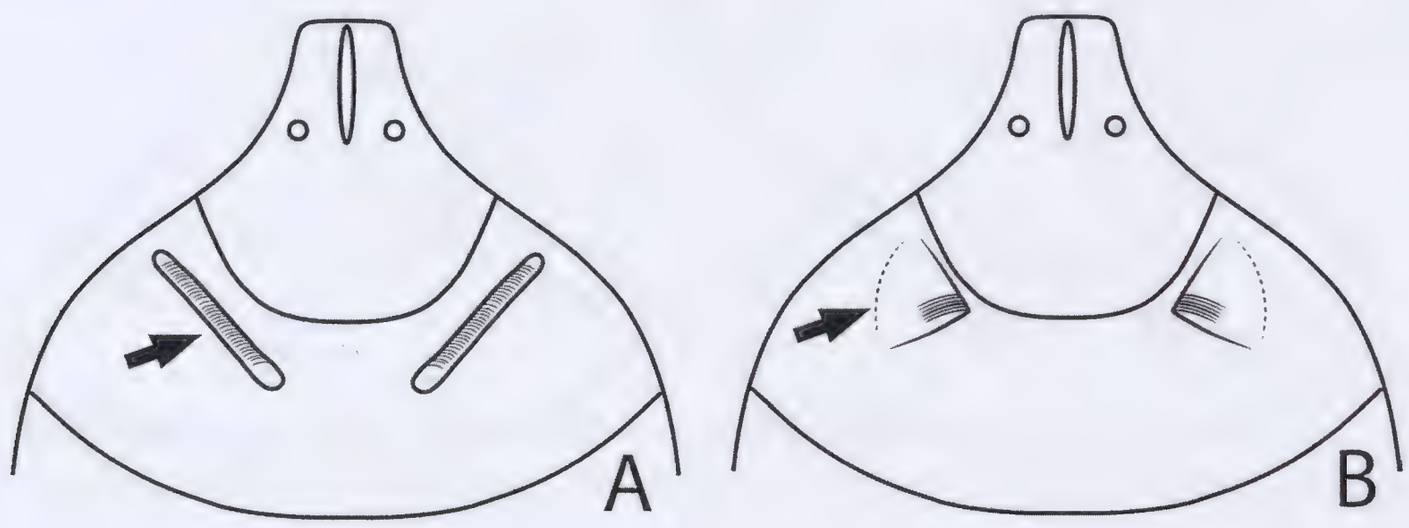
17. Tergal processes with tufts of setae in conspicuous lateral pit (A).....18
– Tergal processes with tufts of setae emerging directly from surface without any pit (B) 20



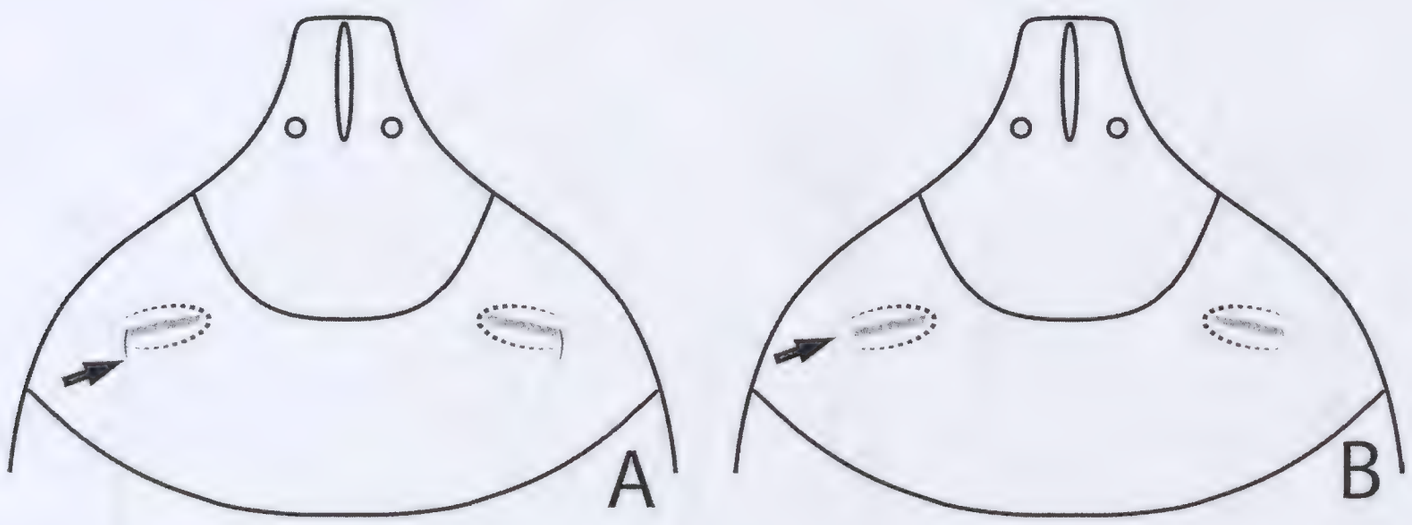
18. Pits of tergal processes subcircular with inner part covered by translucent integument, so that hole is hemispheric (A).....*hemisphaericus* (C.1)
– Pits of tergal processes fully exposed, not partially covered by any expansion (B) 19



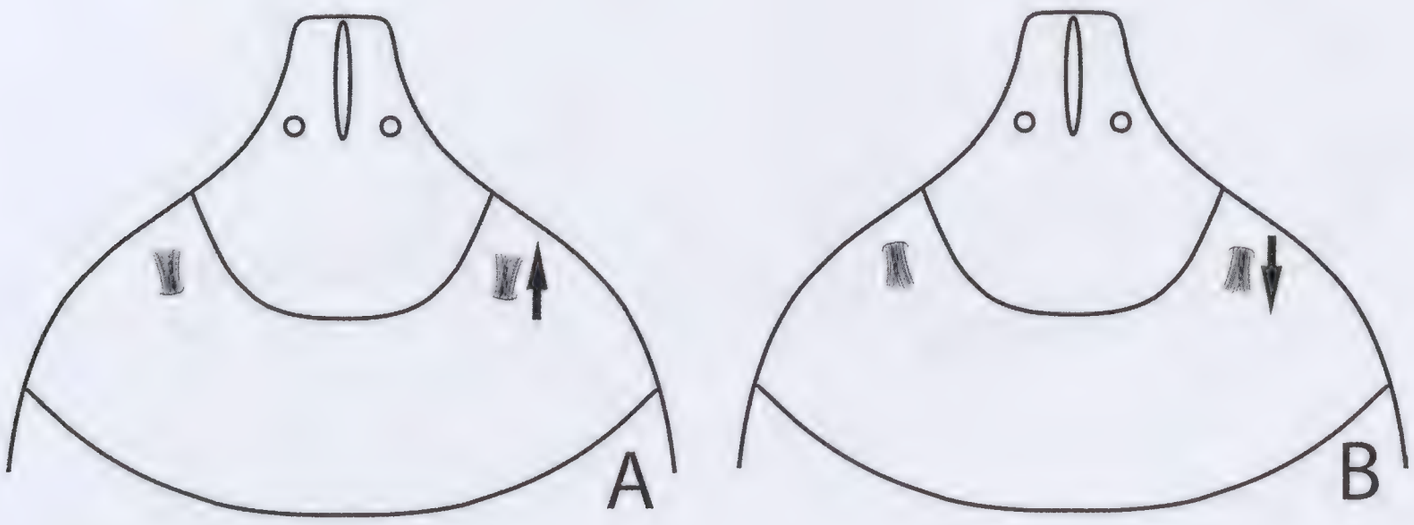
19. Pits of tergal processes elongate, inclined and deeply slit (A) .....*lamellatus* (C.2)
– Pits of tergal processes circular in subtriangular depression (B).....*rettenmeyeri* (C.3)



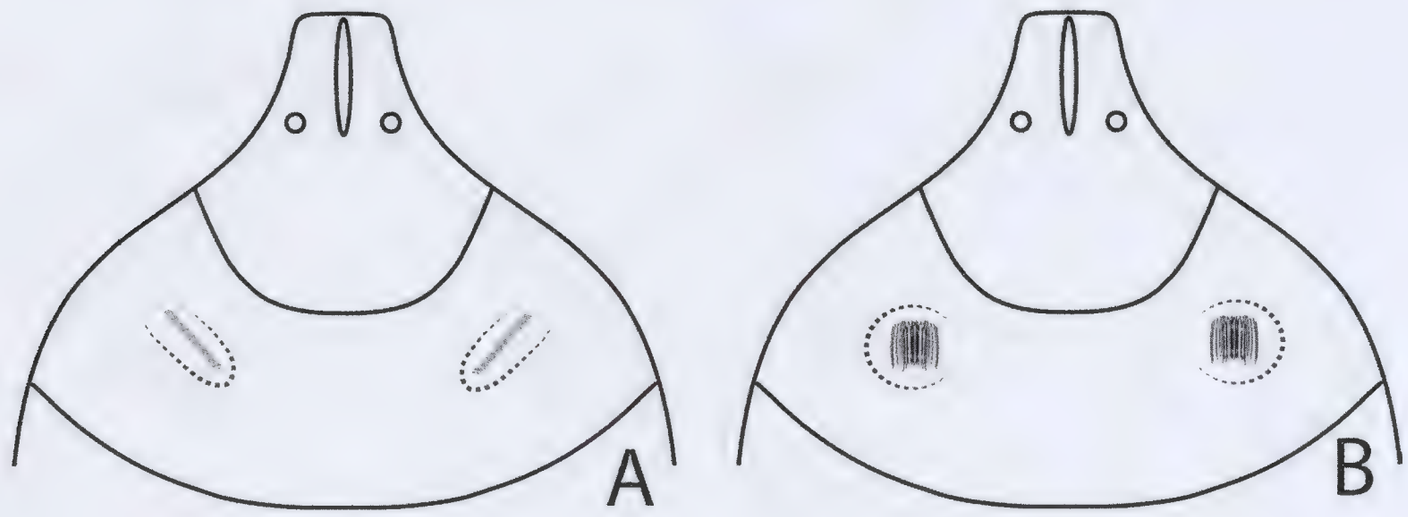
20. Tufts of setae of tergal processes each with one lateral seta distinctly longer than regular ones (A) ..*gilvipes* (D.6)
– Tufts of setae of tergal processes without such distinctly longer seta (B).....21



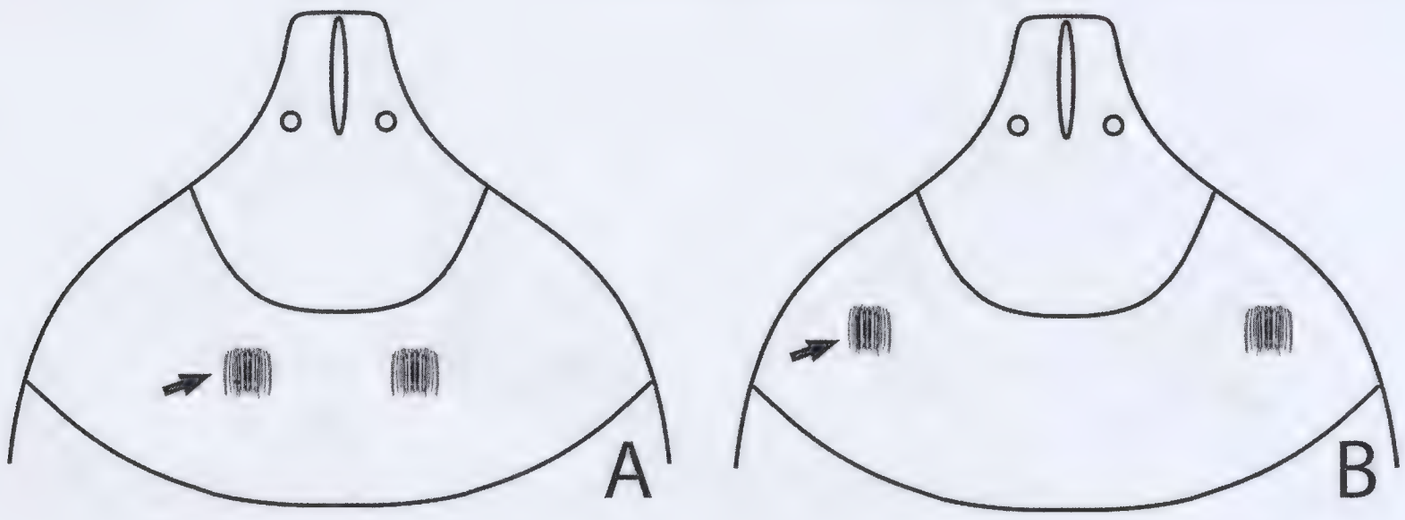
21. Tufts of setae of tergal processes entirely directed anterad (A) .....*amana* (D.1)
– Tufts of setae of tergal processes directed posterad (B) 22



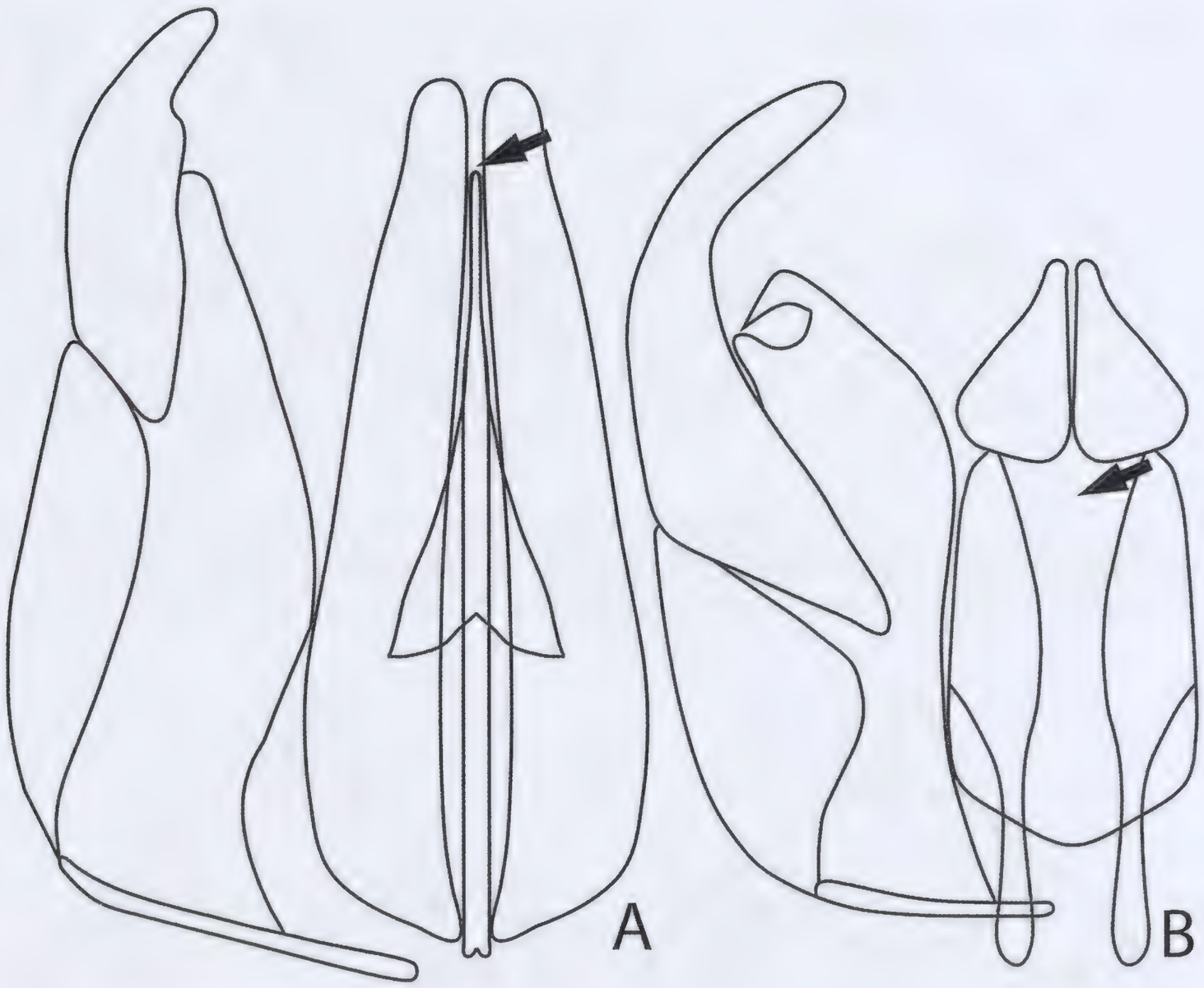
22. Tufts of setae of tergal processes inclined and linear (A)..... *rufipalpis* (D.9)
– Tufts of setae of tergal processes usually circular, but never linear (B).....23



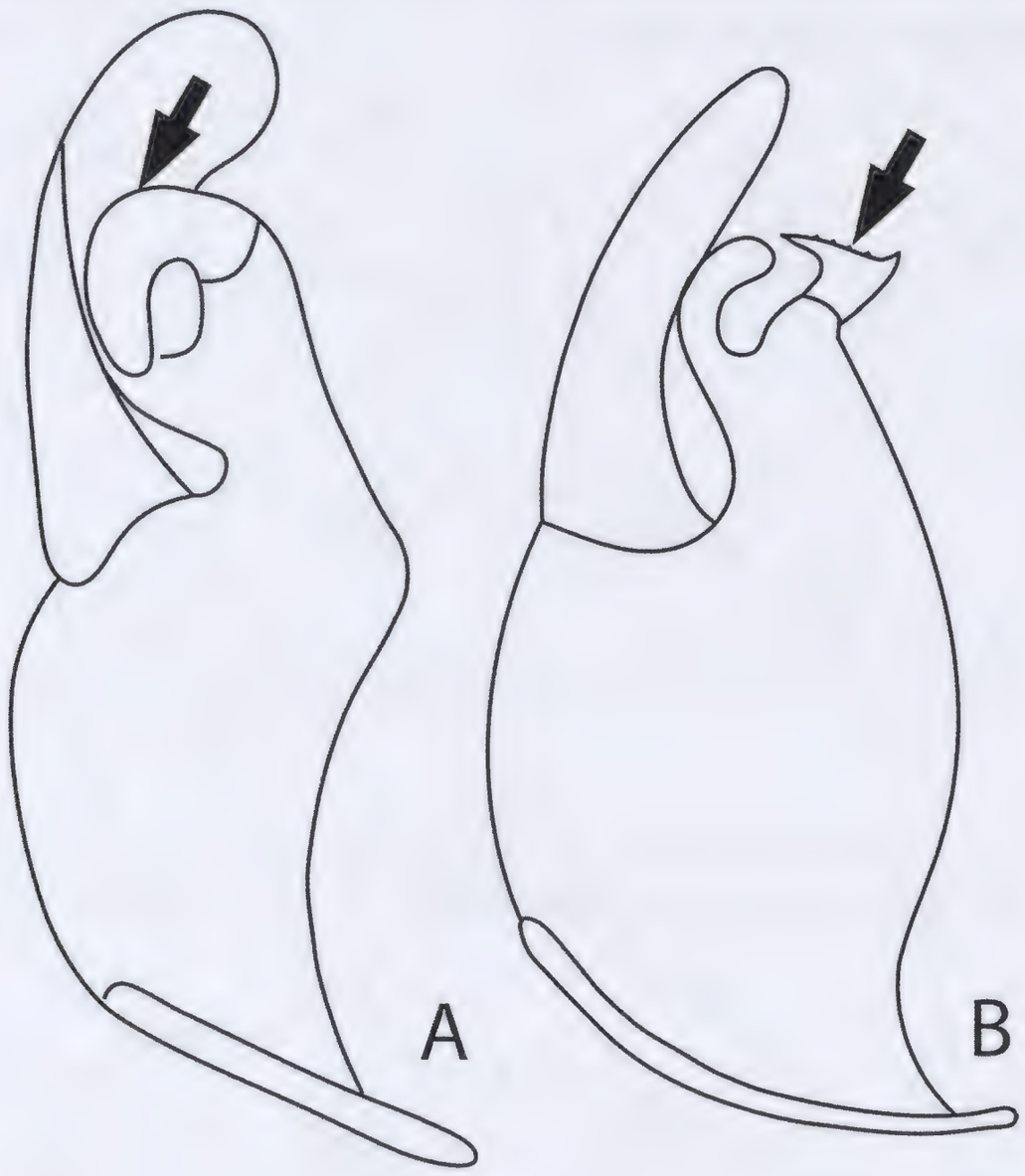
23. Tergal processes located at border between median and lateral thirds of tergal width (A).....24
– Tergal processes located on lateral third of tergal width (B).....25



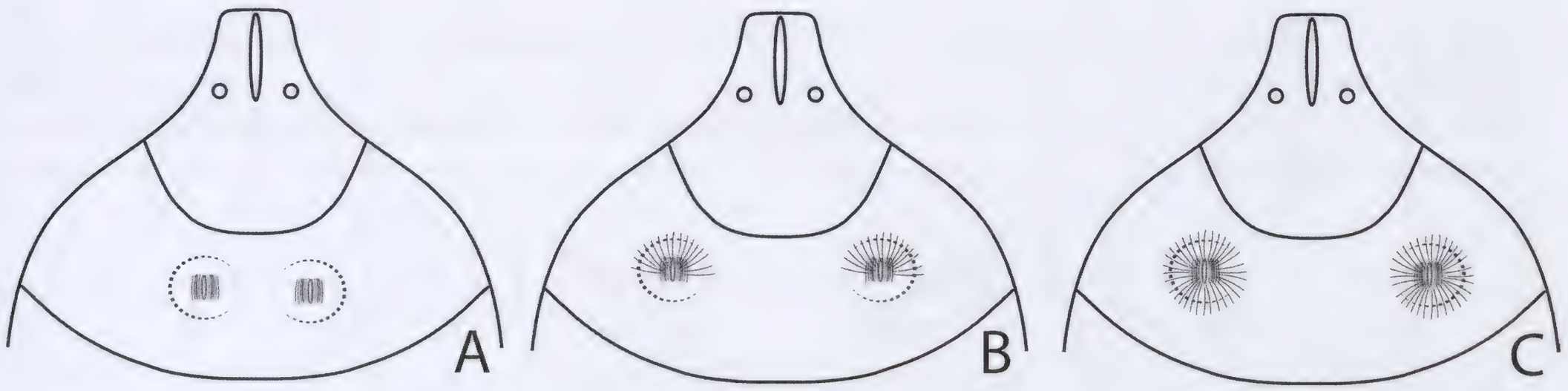
24. Aedeagal dorsal body with elongate median filament; harpe not prominently projected antero-dorsally (A) .... *punctatus* (D.8)
– Aedeagal dorsal body without filament; harpe prominently projected antero-dorsally (B)..... *cornutus* (D.3)



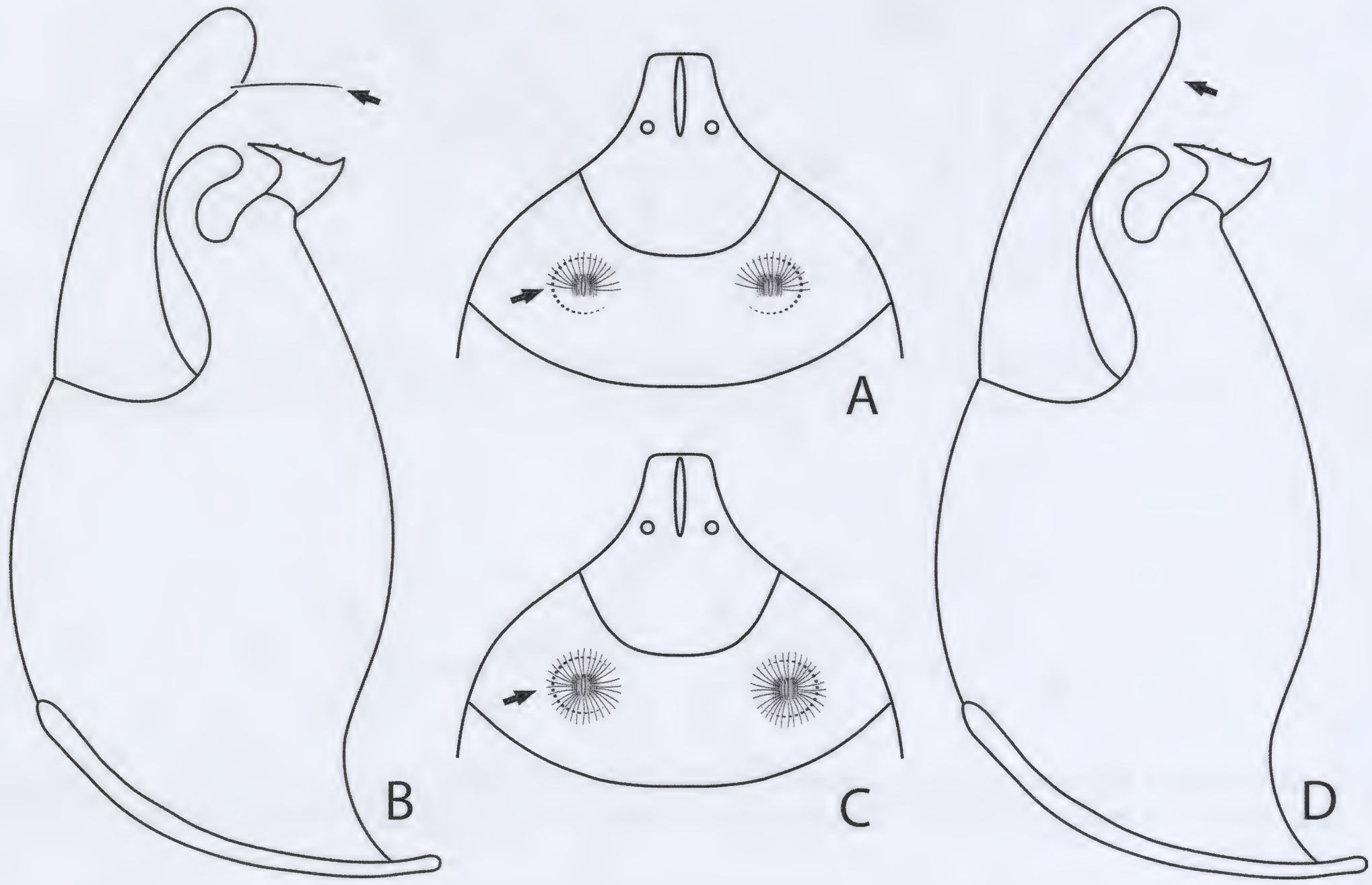
25. Digitus stout, posterior surface including inner corner smooth and without any denticulation (A) ..... *napo* (D.7)
– Digitus not stout, posterior surface serrated, inner corner sharpened (B) 26



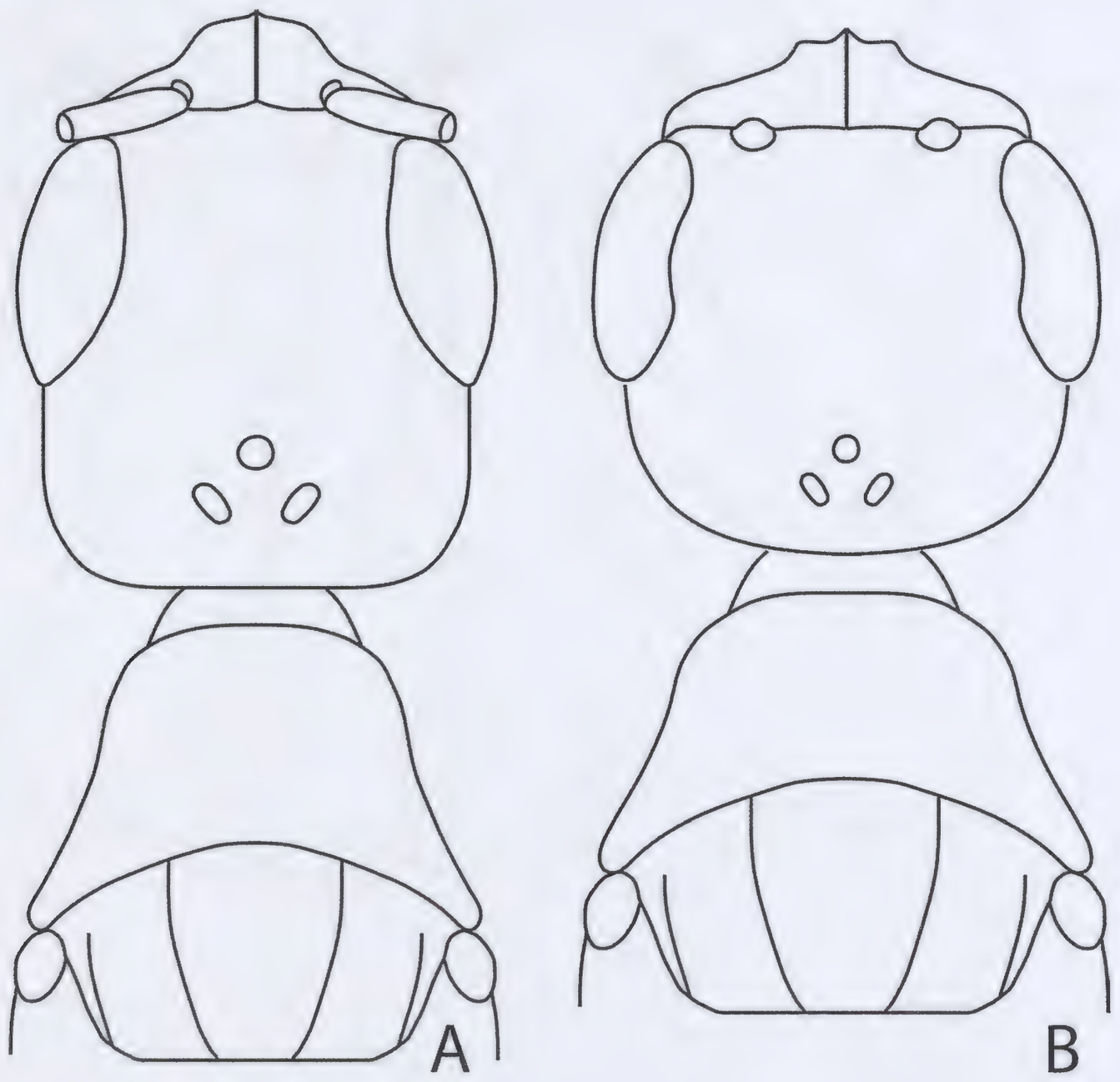
26. Tufts of setae of tergal processes not covered by any set of setae at all (A) ..... *confusus* (D.2)
– Tufts of setae of tergal processes at least partially covered by set of longer anterior setae directed posterad (B, C) 27



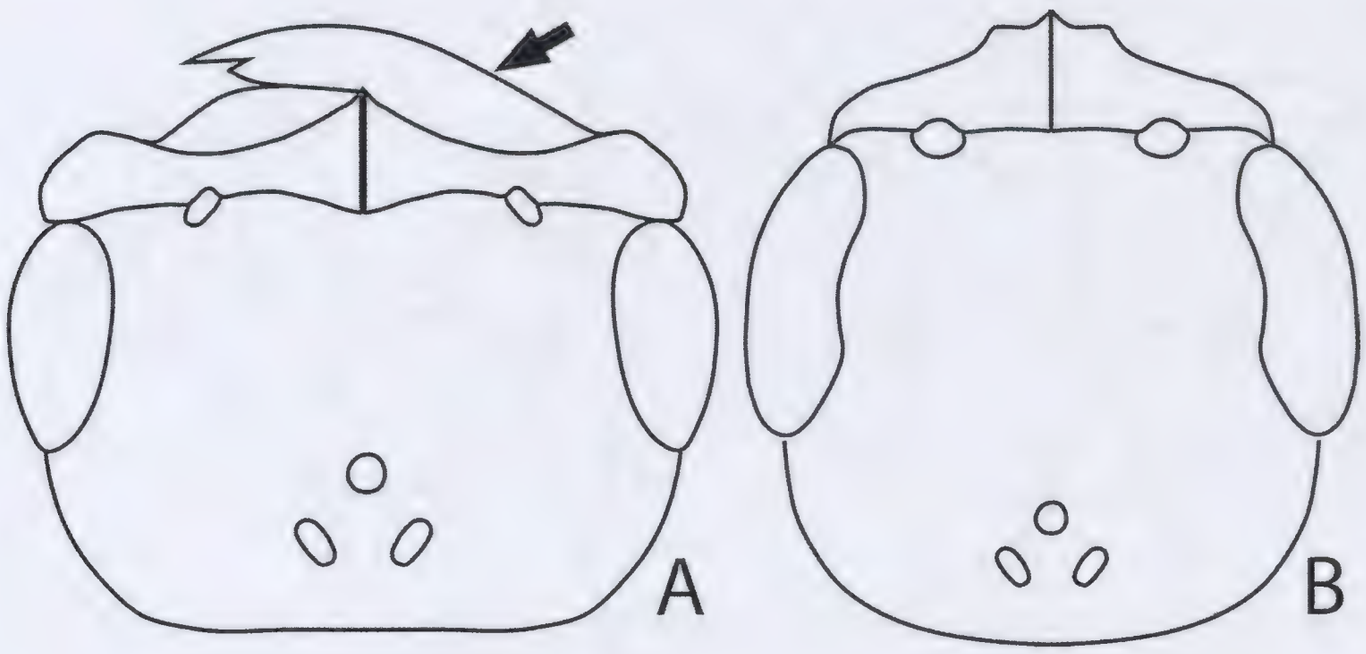
27. Tufts of setae of tergal processes directed posterad, and covered only partially by anterior set of setae, directed posterad (A); inner harpe surface with distinct apical seta (B) ..... *coronatus* (D.3)
– Tufts of setae of tergal processes directed mesad, and fully covered by circular set of setae directed mesad (C); inner harpe surface without distinct apical seta (D) ..... *fungosus* (D.5)



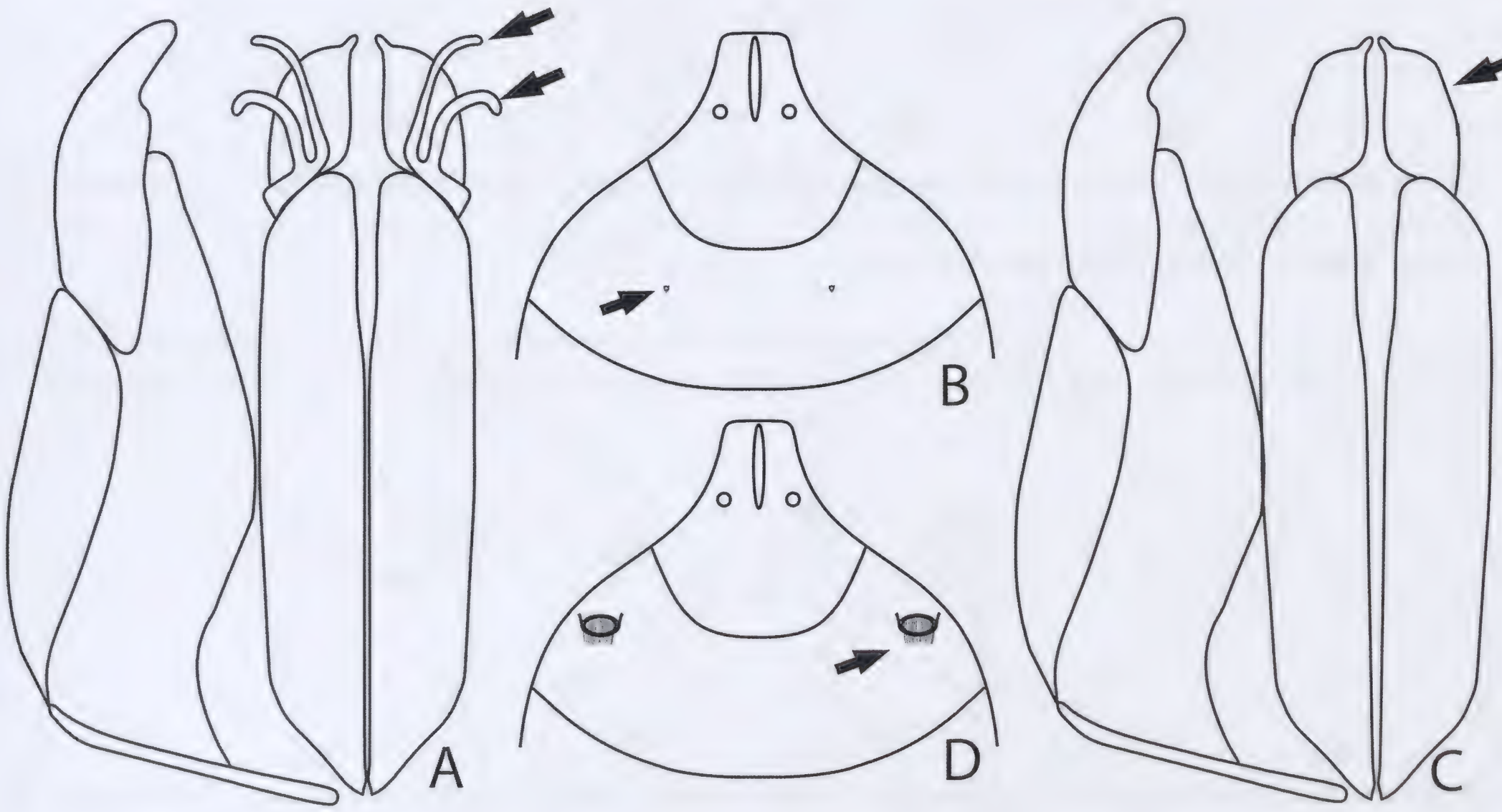
28. Body very elongate; head much longer than wide; dorsal pronotal area nearly as long as mesoscutum, when measured medially (A) ..... *dumosus* (E.4)
– Body not so elongate; head most as long as wide; dorsal pronotal area much shorter than mesoscutum, when measured medially (B).....29



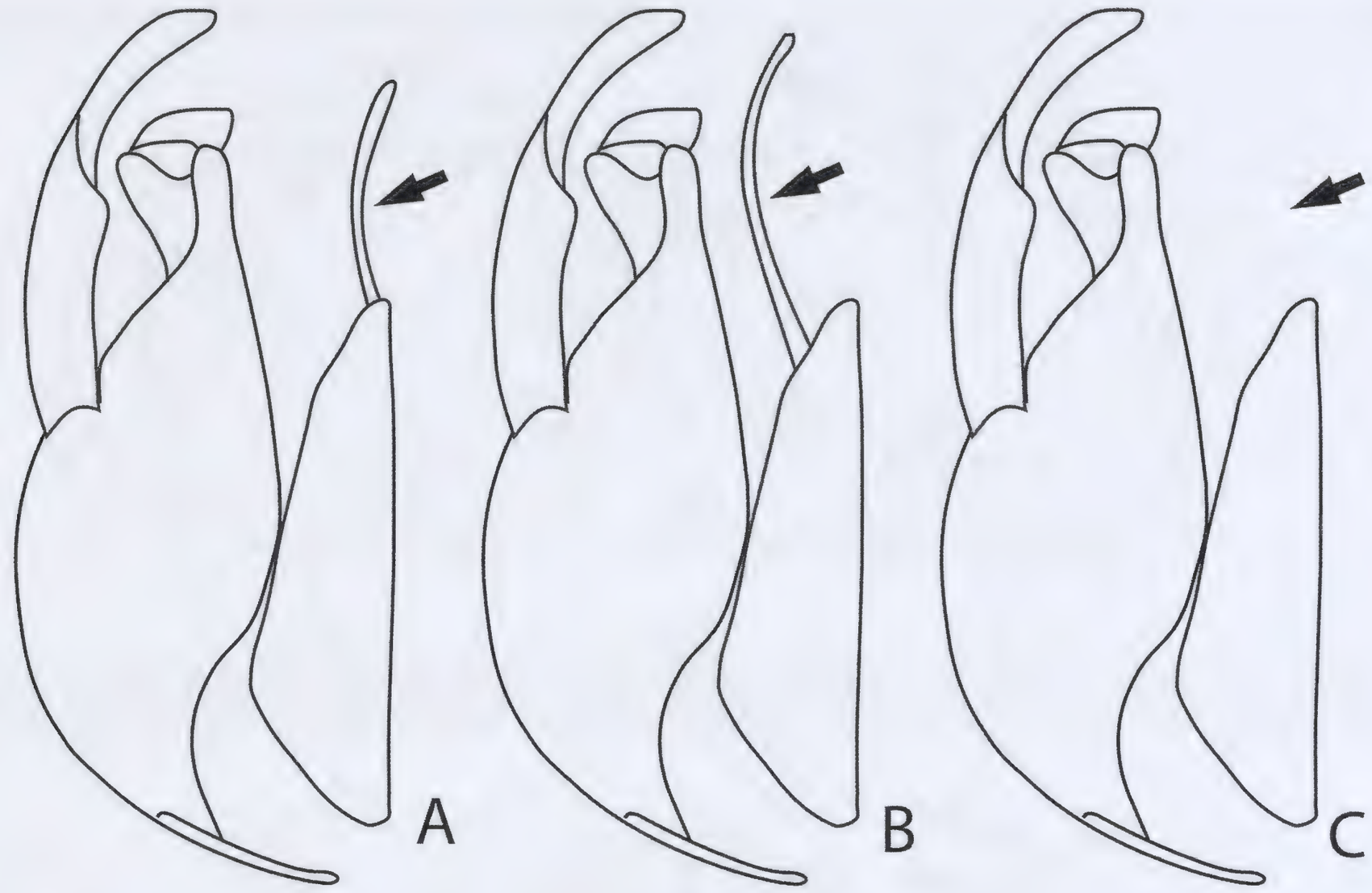
29. Mandibles unusually long, at least ~0.75 × as long as distance between their bases; head much wider than long (A).....*laticephalus* (E.7)
– Mandibles not so long, overlapping each other just little bit when closed; head about as long as wide (B) 30



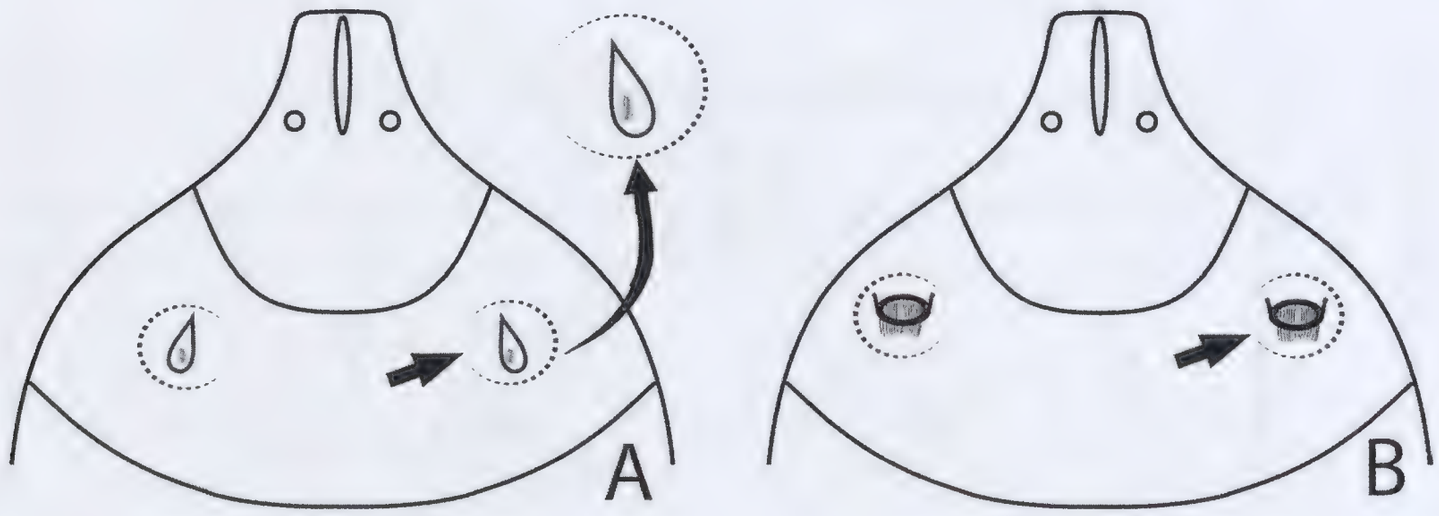
30. Tubercles of tergal processes tiny (A); aedeagal dorsal body with two pairs of flagellae (B) ..... *incomptus* (E.6)
– Tubercles of tergal processes small to large (C); aedeagal dorsal body without such flagellae (D) 31



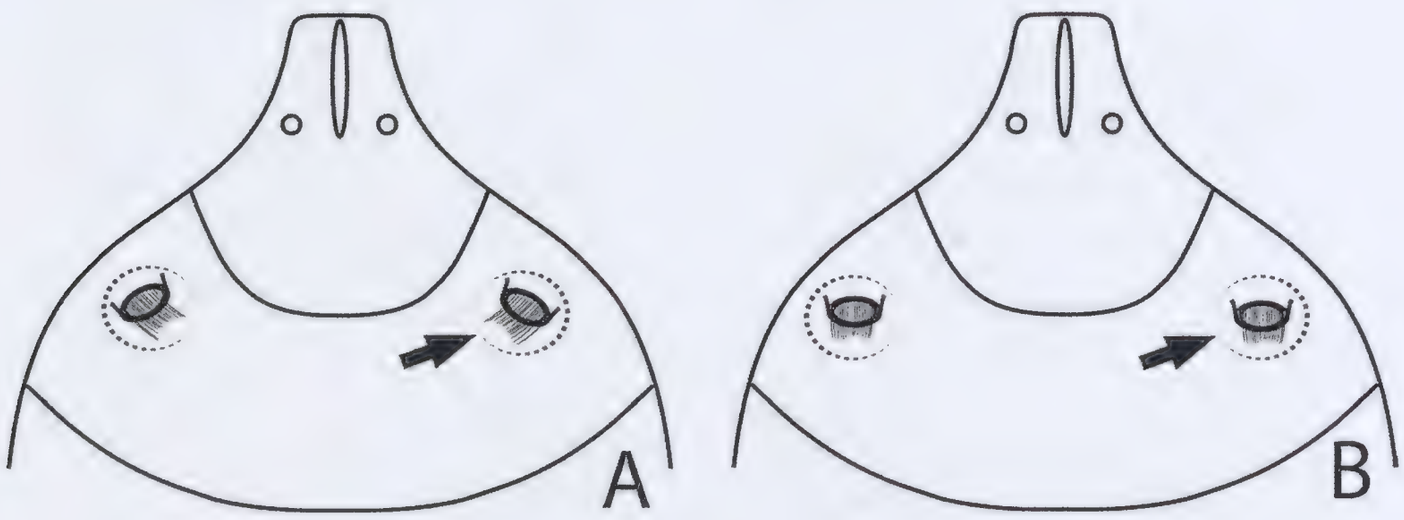
31. Apex of aedeagal ventral ramus with very thin and long filament (A, B).....*microstictus* (E.8)
– Apex of aedeagal ventral ramus without such filament (C) 32



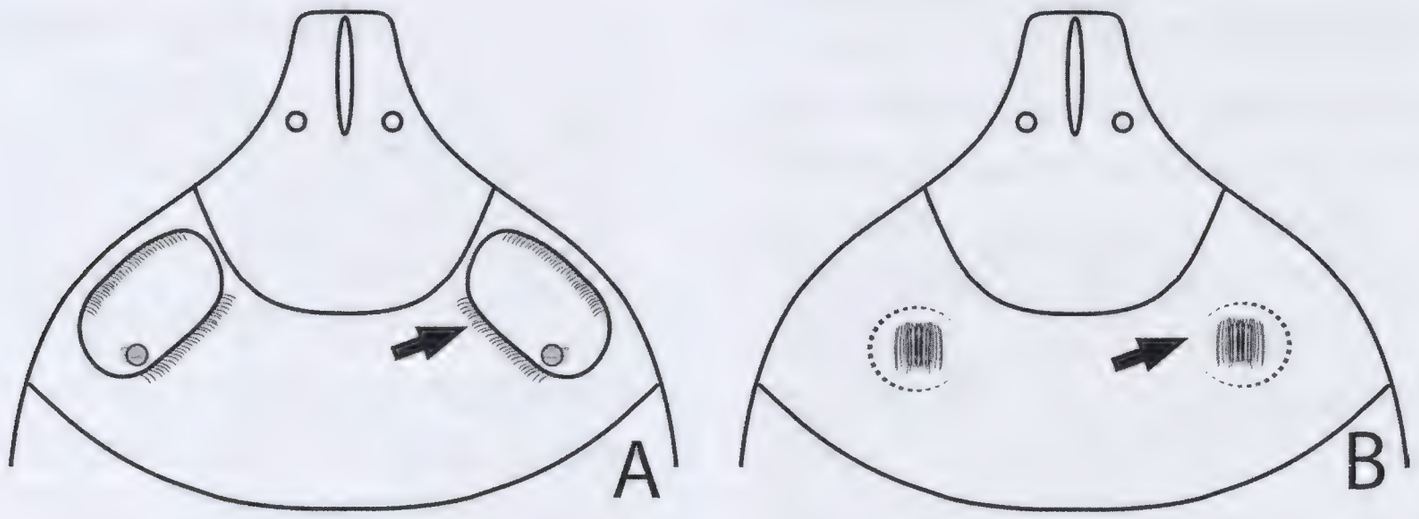
32. Tergal processes with lateral drop-shaped pits, with high rim, sharply pointed anteriorly and rounded posteriorly (A).....*guttus* (E.5)
– Pits of tergal processes never drop-shaped (B).....33



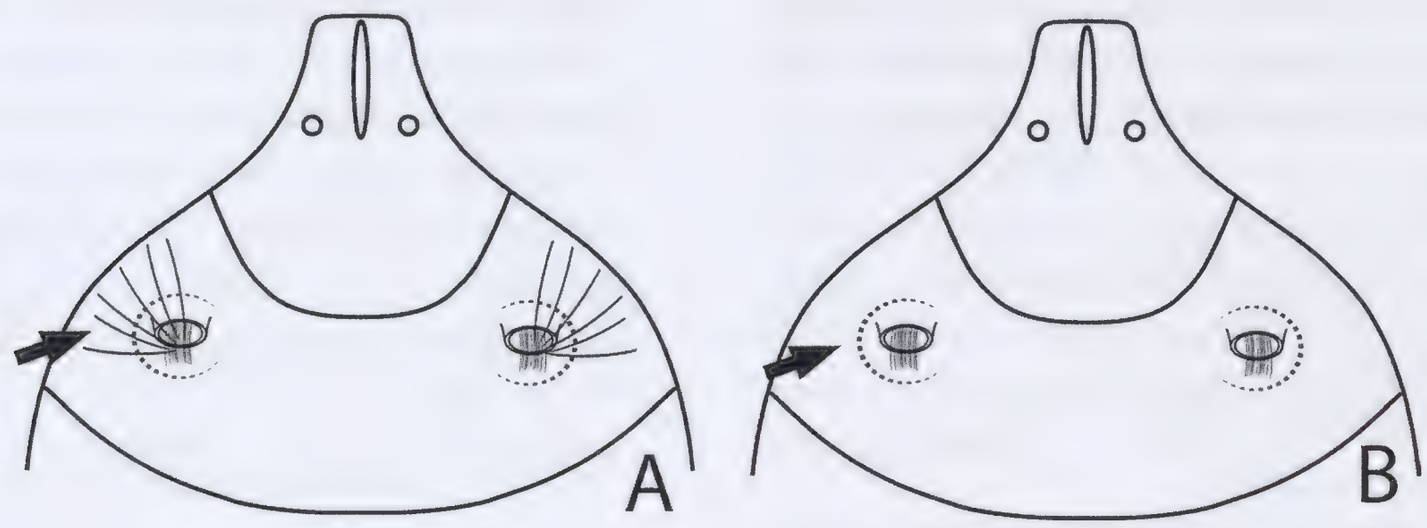
33. Tubercles and tufts of tergal processes at least slightly directed towards each other (A) .....*tuberculatus* (E.11)
– Tubercles of tergal processes not directed towards each other (B) 34



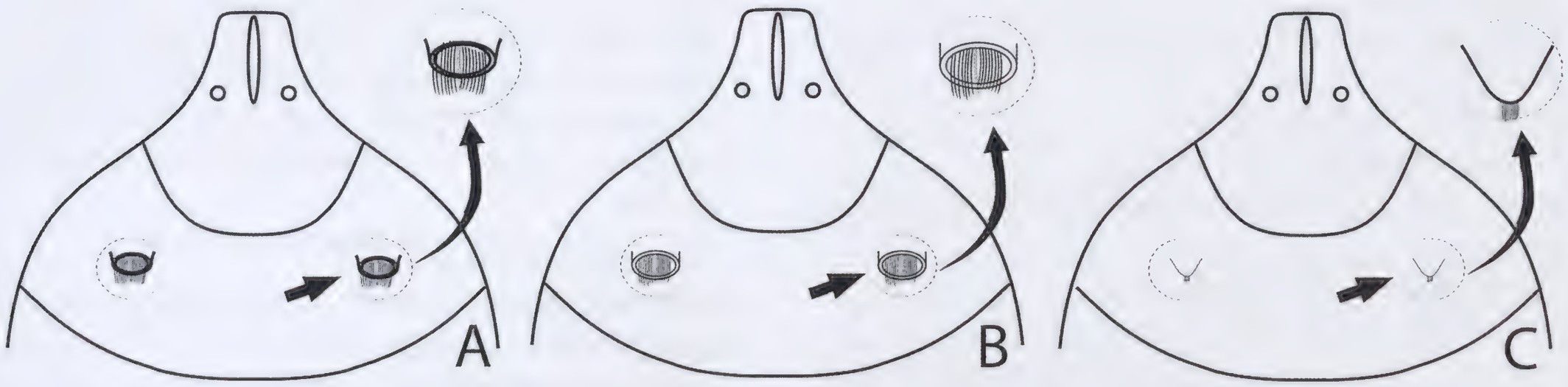
34. Tergal processes very large, occupying more than two thirds of tergal length, and with deep concavity (A) .... *bicavatus* (E.1)
– Tergal processes small or with mid-sized depression, occupying less than half of tergal length, (B) 35



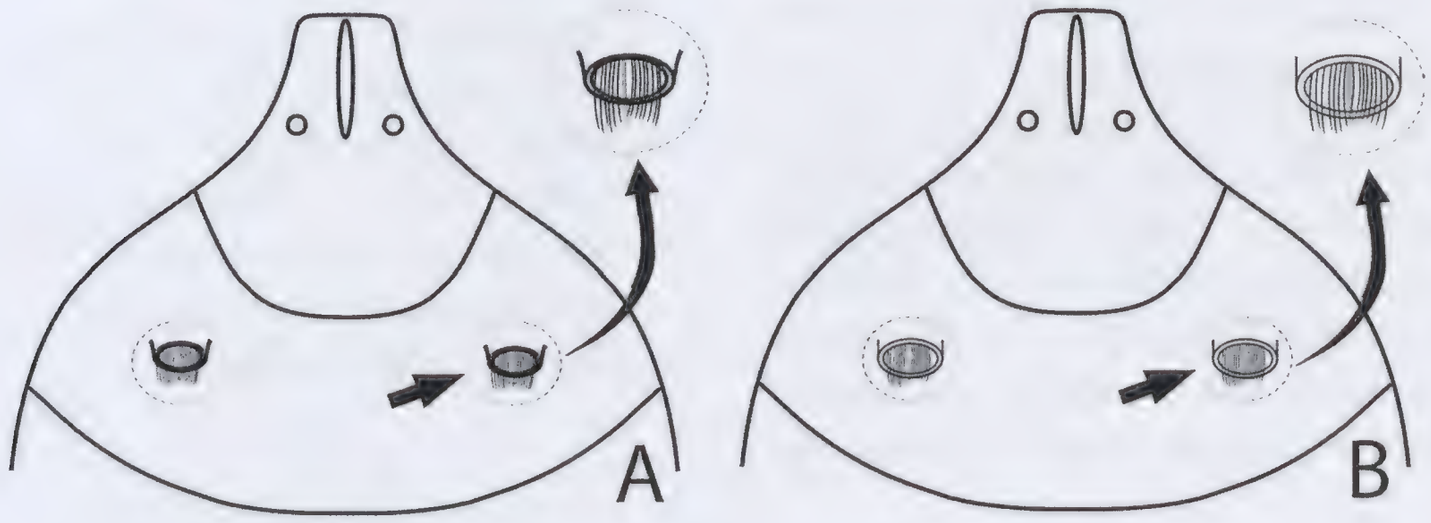
35. Antero-lateral area of depression of tergal process with conspicuous and long set of setae (A) .....*setosus* (E.10)
– Metasomal tergite II without such set of long setae (B).....36



36. Tubercles mostly crater-shaped, tops with pit and tuft of setae (A, B) 37
– Tubercles callus-shaped, progressively narrowing apicad, conical in lateral view, tops without pit, but with tuft of setae (C)..... *chiapanus* (E.2)



37. Tubercles navel-shaped, with highly raised and rounded rim, pits usually densely setose, tufts covering pits (A) .. .. *conicus* (E.3)
– Tubercles ring-shaped, with low raised and sharply edged rim, pits usually wide and tufts usually not covering pits (B)..... *secretus* (E.9)



The species groups

A. *Species group without tergal process*

A.1. *amplus* species-group

This group is the result of the fusion of *amplus* and *dissomphaloides* species-groups. The *dissomphaloides* species-group was proposed by Evans (1963) to accommodate two species "remarkably *Dissomphalus*-like" (in his words), because the aedeagus is divided in ventral rami and dorsal body. However, he allocated these species in *Apenesia* Westwood because of the absence of a tergal process. Alencar *et al.* (2018) transferred this group to *Dissomphalus* based on molecular and morphological phylogenetic analyses.
This group joins all species without tergal processes on the metasomal tergite II, whose genitalia do not have any filament on the aedeagal ventral ramus as in the *microstictus* species-group, and no apical flagellae on the aedeagal dorsal body as in *incomptus* species-group.

Check list, 17 species:
amplus Redighieri & Azevedo, 2006
asfartus Brito & Azevedo, 2017
azagus Brito & Azevedo, 2017
boitata Colombo & Azevedo, 2018
boto Colombo & Azevedo, 2018
caribbeanus (Evans, 1969) from *incertae sedis*
clovisi Colombo & Azevedo, 2016
denticulatus (Evans, 1963) from *dissomphaloides* species group
dissomphaloides (Evans, 1963) from *dissomphaloides* species group
insulanus (Evans, 1969) from *dissomphaloides* species group
iozus Brito & Azevedo, 2017
kuara Colombo & Azevedo, 2016
lilloanus (Evans, 1969) from *dissomphaloides* species group
miriamae Colombo & Azevedo, 2016
pyata Colombo & Azevedo, 2016
pygmaeus (Evans, 1969) from *dissomphaloides* species group
simulatus (Evans, 1969) from *dissomphaloides* species group

B. *Species groups with median tergal process*

B.1. *apertus* species group

The tergal processes of this group consist of tufts of short setae, not longer than the tuft diameter. Some species like *D. megomphalus* Evans and *D. deformis* Evans have the largest tufts of the genus. The depression is always single and median, but the range of variation is wide, it can be deep or shallow, large or small. The harpe of the male genitalia is evenly outcurved, without any denticulation.
Except for *D. parvus*, the male genitalia of this group have the aedeagal ventral rami wide and short, much shorter than the aedeagal dorsal body. The inner lobe of the dorsal body is semicircular and has a protuberance directed ventrad, with both inner surface and ventral margin wholly setose.
The new composition of this group is mostly the result of the fusion of the *apertus* and *altivolans* groups.

Check list, 11 species:
albipes (Kieffer, 1904) from *incertae sedis*
altivolans Evans, 1955 [1954] from *altivolans* species-group
apertus Kieffer, 1914
deformis Evans, 1969 from *altivolans* species-group
evansi Azevedo, 1999
isteus Brito & Azevedo, 2017 from *altivolans* species-group
lanceolatus Azevedo, 1999 from *altivolans* species-group
megomphalus Evans, 1969 from *altivolans* species-group
parvus Azevedo, 1999
subdeformis Azevedo, 1999 from *altivolans* species-group
subpilosus Azevedo, 1999

B.2. *bifoveatus* species-group

This group is defined on characters of the male genitalia. The aedeagal ventral rami have on the apex an elongated filament, which is strongly angled anterad and ventrad. This feature is unique in the genus. The tergal processes of this group are located in a single depression, which can be very shallow or slightly deep, and occupies the median third of the tergal width or a little more. Inside the depression there is a pair of tufts of setae.

Check list, six species:
angulatus Azevedo, 1999
asitius Brito & Azevedo, 2017
bifoveatus Kieffer, 1906 [1905]
ibocius Brito & Azevedo, 2017
microculus Azevedo, 1999
tisinus Brito & Azevedo, 2017

B.3. *bisulcus* species-group

The tergal processes of this group consist of median linear and transverse tufts of setae. These tufts are placed close to each other, almost touching, and located inside a single depression, which occupies the median third of the tergal width, or slightly more. This depression is so shallow that it is difficult to distinguish from the tergal surface.

Check list, two species:
bisulcus Ashmead, 1894
horizontalis Azevedo, 1999

B.4. *brasiliensis* species-group

This group is defined on characters of the male genitalia. That is because the aedeagus has two features which are very unusual and unique in *Dissomphalus*. The aedeagal ventral rami are tubular, with a circular cross-section or nearly so, and the aedeagal dorsal body is noticeably short, with its apex anterior to the base of the digitus (Redighieri & Azevedo, 2006). The clypeus is broadly projected forward, so that the median lobe is not as clearly defined as in the *gilvipes* species-group, for example.
The tergal processes of this group are placed in shallow median depressions. Each depression has a small, tufted navel-shaped tubercle. The species of this group have a small body, with a delicate metasoma, which usually collapses when the specimen is dry pinned. In this case, the depressions seem to be fused into a single one.

Check list, two species:
brasiliensis Kieffer, 1910
tubulatus Redighieri & Azevedo, 2006

B.5. *curvifoveatus* species-group

The tergal processes of this group consist of very large median pits, strongly arched inward medially, totally covered by a lot of long setae directed mesad and posterad. These pits are located in a single median depression, which occupies the median third of the tergal width. This depression is deep, wide and somewhat triangular (Azevedo, 1999).

Check list, one species:
curvifoveatus Azevedo, 1999

B.6. *linearis* species-group

The tergal processes of this group are placed in a single depression. This depression is large and embraces broadly the posterior margin of metasomal tergite I, so that it has a half-moon shape in dorsal view (Azevedo, 1999), like in the *rasissimus* species-group. However here the depression is somewhat deep and occupies slightly more than the median third of the tergal width. Another important difference is that *linearis* does not have tubercles, whereas in *rasissimus* the tubercles are present, although not clearly defined. In one species the posterior margin is missing, so that it seems an open depression. Nevertheless, this aspect should not be interpreted as a double depression.

Check list, three species:
completus Azevedo, 1999
incompletus Azevedo, 1999
linearis Azevedo, 1999

B.7. *longiclypeus* species-group

The tergal processes of this group consist of navel-shaped tubercles, located in a single transversally elliptical depression, which occupies the median third of the tergal width. The tubercles are located medially, far from the edge, so that they do not modify the margin of the depression.

Check list, five species:
gigantus Azevedo, 1999
longiclypeus Azevedo, 1999
multicoriaceus Azevedo, 1999
scamatus Azevedo, 1999
serratus Azevedo, 1999

B.8. *rasissimus* species-group

The tergal processes of this group are placed in a single depression. This depression is large and embraces broadly the posterior margin of metasomal tergite I, so that it has a half-moon shape in dorsal view (Azevedo, 1999), like in the *linearis* species-group. However here the depression is very shallow to such an extent that is hardly observable and occupies almost the two median thirds of the tergal width. Besides, the male genitalia have the harpes deeply divided medially, forming two distinct lobes.

Check list, two species:
bilobatus Azevedo, 1999
rasissimus Azevedo, 1999

B.9. *ulceratus* species-group

The tergal processes of this group are placed in a single depression. This depression occupies the median third of the tergal width or even more. It is elliptical, biconcave or subcircular, and can be shallow, but occasionally conspicuous (Azevedo 1999). The depression has a pair of tufts with short setae, not longer than their diameter. The tufts display a wide range of variation, they can be circular, elliptical, small or large.
The harpes of the male genitalia have a peculiar shape, their apices have corners that are produced and angulate, the apical margin is truncate or dentate, and the base is wide. Analyzing the harpes is the easiest way to recognize the group.

Check list, six species:
concavatus Azevedo, 1999
congo Colombo & Azevedo, 2016
dentiformis Azevedo, 1999
rectilineus Azevedo, 1999
terbius Brito & Azevedo, 2017
ulceratus Evans, 1969

B.10. unitus species-*group*

The tergal processes of this group are located in a single depression. This depression occupies the median third of the tergal width. It is elliptical or subcircular, only slightly deep, and almost totally covered by a pair of joined tufts of long setae directed posterad (Azevedo, 1999), longer than the diameter of each tuft. The *apertus* species-groups have a similar pattern, but here the depression is smaller, and the setae of tufts are much longer.

Check list, two species:
delgatus Azevedo, 1999
unitus Azevedo, 1999

B.11. *vallensis* species-group

The tergal processes of this group consist of median tubercles, located in a single elliptical or subcircular depression, which occupies the median third of the tergal width. The tubercles are located laterally close to the margin, so that they are slightly or strongly directed mesad. Because of that, the depression seems to be biconcave in dorsal view. The tubercles are not exactly navel-shaped because their base is conical and only the apex is somewhat evenly wide, then it should be more appropriate to treat them as subnavel-shaped.
The clypeus has one or three median teeth. The male genitalia are complex, the aedeagal dorsal lobe is richly ornamented, and the base of several species is also ornamented with filaments or dentition.
The new composition of this group is the result of the fusion of the *vallensis*, *stellatus* and *basidentatus* groups.

Check list, 20 species:
basidentatus Azevedo, 1999 from *basidentatus* species-group
bicarinatus Azevedo, 1999 from *stellatus* species-group
bifurcatus Azevedo, 1999
bisserratus Azevedo, 1999
cerutus Azevedo, 1999 from *basidentatus* species-group
digitatus Azevedo, 1999
dilatatus Azevedo, 1999
extrarramis Azevedo, 1999
largidentatus Azevedo, 1999 from *stellatus* species-group
planus Azevedo, 1999
polidentatus Azevedo, 1999
rosangelae Colombo & Azevedo, 2016
rotundus Azevedo, 1999 from *basidentatus* species-group
scavatus Azevedo, 1999 from *stellatus* species-group
stellatus Azevedo, 1999 from *stellatus* species-group
strictus Azevedo, 1999
torem Colombo & Azevedo, 2018
tortuosus Azevedo, 1999 from *stellatus* species-group
triangularis Azevedo, 1999
vallensis Evans, 1979

C. *Groups with lateral pitted process*

C.1. *hemisphaericus* species-group

The tergal processes of this group consist of lateral pitted modifications with a tuft of setae, but never have any tubercle. The pits of this group are large and elliptical because their inner part is covered by a translucent sclerite, so that the hole is hemispheric, which makes the group easily recognized (Azevedo, 2003).

Check list, six species:
ferocus Azevedo, 2003
fredi Colombo & Azevedo, 2016
gordus Azevedo, 2003
hemisphaericus Azevedo, 2003
undatus Azevedo, 2003
vampirus Azevedo, 2003

C.2. *lamellatus* species-group, new

The tergal processes of this group consist of lateral pitted modifications with a tuft of setae, but never has any tubercle. The main character of this group is that the pit is very deep, elongated, and with an inclined slit. This slit is unique in *Dissomphalus*.

Check list, three species:
collaris Evans, 1962 from *incertae sedis*
lamellatus Redighieri & Azevedo, 2006 from *incertae sedis*
ubracus Brito & Azevedo, 2017 from *incertae sedis*

C.3. *rettenmeyeri* species-group, new

The tergal processes of this group consist of lateral pitted modifications with a tuft of setae, but never has any tubercle. The pits of this group are somewhat circular or nearly so, their opening is subvertical. The pits are located in an opened subtriangular depression, with the vertex located medially and the outer margin outcurved and opened. The combination of characteristics is unique in the genus.

Check list, one species:
rettenmeyeri Evans, 1964 from *incertae sedis*

D. *Species-groups with lateral tufted process*

D.1. *amana* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle and pits. The main character of this group is that the setae of tufts are directed anterad, which is unique in the genus. The tufts are located inside a depression (Colombo & Azevedo, 2016).

Check list, two species:
amana Colombo & Azevedo, 2016
potyra Colombo & Azevedo, 2016

D.2. *confusus* species-group, new

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts are composed by short setae. This character seems to be not strong enough, so that it should be a waste basket of those groups with lateral tufted processes. However, it is useful for alpha taxonomic purposes.
Some species, such as *Dissomphalus clypeatus* Evans, were described as having a tiny pit, but Azevedo (2003) examined its holotype and was not able to see any pit. Such tiny pits can cause a misinterpretation of key couplet 19. However, to follow the first entrance the pits have to be conspicuous. *Dissomphalus taiabocu* Colombo & Azevedo seems to have this issue.

Check list, four species:
abarus Brito & Azevedo, 2017 from *incertae sedis*
clypeatus Evans, 1955 [1954] from *incertae sedis*
confusus Ashmead, 1894 from *incertae sedis*
taiabocu Colombo & Azevedo, 2016 from *incertae sedis*

D.3. *cornutus* species-group, new

The tergal processes of this group consist of tufted modifications, without any tubercle or pit. The tufts are located between the median and lateral thirds of the tergal width. Because of that, key couplet 5 can cause misinterpretations, but considering that the tergal processes are not located within the median third of the tergal width, this group is regarded as having lateral processes. The surface of metasomal tergite II is flat, without any depression. The tufts have few and long setae compared with the average found in the genus. In the male genitalia, the harpe is strongly projected antero-dorsally.

Check list, three species:
cornutus Evans, 1964 from *incertae sedis*
fimbriatus Redighieri & Azevedo, 2006 from *incertae sedis*
scopatus Redighieri & Azevedo, 2004 from *incertae sedis*

D.4. *coronatus* species-group

The tergal processes are characterized by having a pair of tufts with setae directed posterad, without any tubercle pit. Each tuft is located inside a conspicuous depression. This depression has also setae directed posterad circulating its anterior board, so that it partially covers the tufts. Another important character is the presence of a distinct seta on the inner surface of the harpe in the male genitalia. This group is similar to the *fungosus* species-group (see it for details).

Alencar & Azevedo (2006) defined this group based on the presence of a crown-like structure on the aedeagal dorsal body. However, such structure is present in most of the species of *Dissomphalus*, it is placed on the base of the aedeagal dorsal body, which supports the apical lobe. Thus, it does not work for diagnosing any group.

Check list, 14 species:
aculeatus Alencar & Azevedo, 2006
afestus Brito & Azevedo, 2017
auritus Alencar & Azevedo, 2006
coronatus Alencar & Azevedo, 2006
culteratus Alencar & Azevedo, 2006
declinatus Alencar & Azevedo, 2006
decussatus Alencar & Azevedo, 2006
flexuosus Alencar & Azevedo, 2006
hirtus Alencar & Azevedo, 2006
galeatus Alencar & Azevedo, 2006
pronus Alencar & Azevedo, 2006
ramosus Alencar & Azevedo, 2006
sinatus Alencar & Azevedo, 2006
uber Alencar & Azevedo, 2006

D.5. *fungosus* species-group, new

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. They are characterized by having a tuft of setae converging mesad. Each tuft is located inside a conspicuous depression, which has setae circulating its board. This group is similar to the *coronatus* species-group (Alencar & Azevedo 2006), because both groups have the setae circulating the board of the depression. However, in the former the setae circulate all of the board, whereas in the latter they circulate only the anterior half of the board. Another difference in the tergal processes is related to the orientation of the setae. Both sets of setae of the tufts and the depression are mesad in the former, whereas they are directed posterad in the latter.
In the genitalia, the inner harpe surface of the *coronatus* species-group has a distinct seta directed mesad or nearly so. This seta is absent in the *fungosus* species-group.

Check list, one species:
fungosus Evans, 1979 from *incertae sedis*

D.6. *gilvipes* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts of the tergal processes can be somewhat circular or even a little elongated, but almost always have the most lateral seta distinctly longer than others, which is the most important diagnostic character of this group. In addition, the clypeus is broadly projected forward, so that the median lobe is not clearly defined (Azevedo, 2003).

Check list, six species:
alticlypeatus Azevedo, 2003
arbeius Brito & Azevedo, 2017
bicerutus Azevedo, 2003
gilvipes Evans, 1979
irupe Colombo & Azevedo, 2018
krombeini Azevedo, 1999

D.7. *napo* species-group, new

The tergal processes of this group consist of a lateral tufted modifications, without any tubercle or pit. The male genitalia have the digitus stout, large, with the posterior surface without denticulation and the inner corner on the posterior margin without any protuberance, so that the posterior surface is wholly and evenly convex. The digitus also has the distal tip narrowly rounded, but not sharp. All these characteristics in the digitus are unique among the American species. Its single species was placed at the *punctatus* species-group, because of the similarity of the tergal processes. However, the tergal processes in the *napo* species-group are much more lateral than in the *punctatus* species-group.

Check list, one species:
napo Evans, 1979 from *punctatus* species-group

D.8. *punctatus* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts are located between the median and lateral thirds of the tergal width. Because of that, key couplet 5 can cause misinterpretations, but considering that the tergal processes are not located within the median third of the tergal width, this group is regarded as having lateral processes. These characteristics are the same as in the *cornutus* species-group. However, in the former group the tergal processes are located inside a circular depression, with densely setose margins which are not angulate, and setae directed posterad. In addition, the male genitalia have an elongate median filament in the aedeagal dorsal body (Azevedo, 2003).

Check list, six species:
acutipupu Colombo & Azevedo, 2018
bahiensis Redighieri & Azevedo, 2006
cuca Colombo & Azevedo, 2018
jurupari Colombo & Azevedo, 2018
punctatus (Kieffer, 1910)
tupinikim Colombo & Azevedo, 2016

D.9. *rufipalpis* species-group

The tergal processes of this group consist of lateral tufted modifications, without any tubercle or pit. The tufts are located inside an elliptical and inclined depression, and consequently the tufts follow the depression's shape, so that the tufts are clearly linear and oblique. That is the most important diagnostic character of this group (Azevedo, 2003).

Check list, five species:
ellipticus Evans, 1969
guarani Colombo & Azevedo, 2016
inclinatus Redighieri & Azevedo, 2006
infissus Evans, 1969
rufipalpis Kieffer, 1910

E. *Species-groups with lateral tubercled processes*

E.1. *bicavatus* species-group

The tergal processes of this group consist of antero-lateral depressions, which are exceptionally large, usually more than 0.5 × the median length of metasomal tergite II, and usually deep, with the cross-section somewhat subcircular. Each depression has a tufted navel-shaped tubercle located at the medial surface, the inner and outer margins have rows of short setae directed posterad. Such depressions are unique in the genus (Azevedo, 2001).
I have seen many undescribed species with depressions similar to those found in the *bicavatus* species group, but smaller, which can cause confusion.

Check list, 35 species:
abruptus Azevedo, 2001
alticarinatus Azevedo, 2001
archeatus Azevedo, 2001
bicavatus Evans, 1979
basivolsellus Azevedo, 2001
bivolsellus Azevedo, 2001
curvilongus Azevedo, 2001
elongatus Azevedo, 2001
falcatus Evans, 1962
falciformis Azevedo, 2001
flagellatus Azevedo, 2001
geniculatus Azevedo, 2001
gladius Azevedo, 2001
intradentatus Azevedo, 2001
largimanus Azevedo, 2001
latus Azevedo, 2001
lobisserratus Azevedo, 2001
longimerus Azevedo, 2001
longipilosus Azevedo, 2001
mantoides Azevedo, 2001
megadentatus Azevedo, 2001
microdentatus Azevedo, 2001
octavus Azevedo, 2001
pedipalpoides Azevedo, 2001
piscicercus Azevedo, 2001
rectangularis Azevedo, 2001
retorcerens Azevedo, 2001
sinuatus Azevedo, 2001
spiculus Azevedo, 2001

strepsus Azevedo, 2001
subtriangularis Azevedo, 2001
tetracerutus Azevedo, 2001
tetralobatus Azevedo, 2001
trogon Azevedo, 2001
tropoides Azevedo, 2001

E.2. *chiapanus* species-group, new

The tergal processes of this group consist of lateral tufted callus-shaped tubercles. This kind of tubercles are usually smaller than navel-shaped tubercles, progressively narrowing apicad, so that they have pyramidal features. On the top of each tubercle, a tuft of setae is raising.
Sometimes, it is difficult to distinguish ring- and callus-shaped tubercles because of their small size, as in *D. borus* Brito & Azevedo. In *D. arteobius* Brito & Azevedo, the depressions have setae lateral to them, which can cause confusion with the *setosus* species-group.

Check list, seven species:
arteobius Brito & Azevedo, 2017 from *incertae sedis*
borus Brito & Azevedo, 2017 from *incertae sedis*
caparao Colombo & Azevedo, 2016 from *incertae sedis*
chiapanus Evans, 1962 from *kansanus* species-group
trilobatus Redighieri & Azevedo, 2006 from *incertae sedis*
trisus Brito & Azevedo, 2017 from *incertae sedis*
ilarius Brito & Azevedo, 2017 from *incertae sedis*

E.3. *conicus* species-group

The tergal processes of this group consist of lateral tufted navel-shaped tubercles. The tubercles are located in an inconspicuous depression. This kind of tubercles are evenly wide along their height, with rounded rim, tuft of setae on the top (Azevedo, 2003).
The available information on *D. clausus* Kieffer, *D. flavipes* Kieffer and *D. ocellatus* Kieffer is very poor, but Kieffer (1914b) mentioned the presence of a tergal process that I interpreted as navel-shaped tubercles. I have never examined *D. clausus* and *D. flavipes* Kieffer. Besides, *D. ocellatus* deposited in the Natural History Museum (London, UK) has its metasoma missing. Thus, the placement of these three species at the *conicus* species-group is weakly supported and needs future studies to better understand them.
Three species, *D. archboldi* Evans, *D. nanellus* Evans and *D. isortus* Brito & Azevedo, have their tubercles exceedingly small, and because of that they remind of a ring-shaped style. That can cause confusion. The tubercles of *D. geortus* Brito & Azevedo, *D. mendicus* Evans and *D. peculiaris* Redighieri & Azevedo are even smaller.
Three species, *D. amplexus* Redighieri & Azevedo, *D. caipora* Colombo & Azevedo and *D. differens* Redighieri & Azevedo, have some setae on the antero-lateral surface of metasomal tergite II, which can be interpreted as a character of the *setosus* species-group style. However, in these three species the setae are not thick, as in the *setosus* species-group. Thus, the difference between the *conicus* and the *setosus* species-group is sometimes confusing.

Check list, 38 species:
amplexus Redighieri & Azevedo, 2006 from *incertae sedis*
amplifoveatus Redighieri & Azevedo, 2006 from *incertae sedis*
archboldi Evans, 1969 from *incertae sedis*
ardonius Brito & Azevedo, 2017
arteus Brito & Azevedo, 2017
botocudus Colombo & Azevedo, 2016
caipora Colombo & Azevedo, 2018 from *incertae sedis*
capixaba Colombo & Azevedo, 2016 from *incertae sedis*
cervoides Azevedo, 2003
clausus Kieffer, 1908 from *incertae sedis*
conicus Azevedo, 2003
connubialis Evans, 1966 from *incertae sedis*
curupira Colombo & Azevedo, 2018
curviventris Azevedo, 2003
differens Redighieri & Azevedo, 2006 from *incertae sedis*
elegans Redighieri & Azevedo, 2006 from *incertae sedis*
ettus Brito & Azevedo, 2017
filus Azevedo, 2003
flavipes Kieffer, 1910 from *incertae sedis*
geortus Brito & Azevedo, 2017 from *incertae sedis*
h-ramus Redighieri & Azevedo, 2004
iara Colombo & Azevedo, 2018
ibirapitanga Colombo & Azevedo, 2016 from *incertae sedis*
ibrastus Brito & Azevedo, 2017
isortus Brito & Azevedo, 2017 from *incertae sedis*
laminaris Redighieri & Azevedo, 2004
manus Azevedo, 2003
nanellus Evans, 1969 from *incertae sedis*
ocellatus Kieffer, 1911 from *incertae sedis*
personatus Redighieri & Azevedo, 2006 from *incertae sedis*
racarus Brito & Azevedo, 2017
saci Colombo & Azevedo, 2018
spinosus Azevedo, 2003
teraus Brito & Azevedo, 2017
truncatus Azevedo, 2003
umbilicus Azevedo, 2003
urazius Brito & Azevedo, 2017
verrucosus Redighieri & Azevedo, 2004

E.4. *dumosus* species-group

This group has two main characters. First, the body is elongated, especially the head, with the area posterior to the supra-ocular line very developed. Also, the median clypeal lobe, the dorsal pronotal area and

the metapectal-propodeal disc are elongated. That is unusual because *Dissomphalus* has the body robust (short and wide) in most of its species. This makes the group easily recognizable. Second, the male genitalia have the aedeagal ventral rami very long and the ventral side of the gonostipe much more developed than the dorsal side (Azevedo, 2000). That is unique among species of the genus.

There are two kinds of very distinct tergal processes. One consists of lateral tufted navel-shaped tubercles, both located in a conspicuous depression. Another consists of elliptical lateral depressions with the surface apparently areolate.

Check list, three species:
dumosus Evans, 1966
longicephalus Azevedo, 2003
mirabilis Evans, 1966 from *incertae sedis*

E.5. *guttus* species-group

The tergal processes of this group consist of tufted ring-shaped tubercles. The tubercles are drop-shaped, because they are sharpened anteriorly and rounded posteriorly, so that they resemble a drop. That shape is unique in the genus. Each tubercle has a large pit partially covered by a tuft of setae (Azevedo, 2003).

Check list, two species:
guttus Azevedo, 2003
latimerus Azevedo, 2003

E.6. *incomptus* species-group

The main diagnostic character of this group is in the male genitalia, which have two pairs of flagellae on the aedeagal dorsal body of aedeagus. No other Pan-American species of *Dissomphalus* has such flagellae. The tergal processes of this group are much reduced or even absent (Azevedo, 2003).

Check list, two species:
incomptus Evans, 1964
microtuberculatus Azevedo, 1999

E.7. *laticephalus* species-group

The main diagnostic character of this group is in the head. First, the mandibles are unusually long, at least about 0.75 × as long as the distance between their bases. Second, the vertex of the head is strongly angled or unusually wide. Besides, the head is very wide in comparison with the majority of species in the genus, with its width about 1.2 × its length. The tergal processes of this group are absent or not very conspicuous in size (Azevedo, 2003).

Check list, five species:
contractus Azevedo, 2003
cristatus Redighieri & Azevedo, 2004
laticephalus Azevedo, 2003
lobicephalus Azevedo, 2000
mandibulatus Azevedo, 2003

E.8. *microstictus* species-group

The main diagnostic character of this group is in the male genitalia, which have the apex of the aedeagal ventral ramus with an elongated filament inserted subapically (Alencar & Azevedo, 2008) in the majority of species, and apically only in *D. xanthopus* Ashmead. Thus, the inclusion of this species here broadens the concept of this group. The tergal processes do not only vary among the species, but also intraspecifically. *Dissomphalus microstictus* Evans can have ring- or callus-shaped tubercles, or the tubercles can be even absent (Alencar & Azevedo, 2008). That makes the tergal processes not useful for diagnosing the group.

Check list, 17 species:
balteus Alencar & Azevedo, 2008
divaricatus Alencar & Azevedo, 2008
flaviscapus (Evans, 1969) from *incertae sedis*
forceps Alencar & Azevedo, 2008
incurvatus Alencar & Azevedo, 2008
microstictus Evans, 1969
osseus Alencar & Azevedo, 2008
paululus Alencar & Azevedo, 2008
perparvus Alencar & Azevedo, 2008
perturbatus Alencar & Azevedo, 2008
perventriosus Alencar & Azevedo, 2008
pilus Alencar & Azevedo, 2008
raziogus Brito & Azevedo, 2017
refertus Alencar & Azevedo, 2008
signatus Alencar & Azevedo, 2008
uncus Alencar & Azevedo, 2008
xanthopus Ashmead, 1893 from *xanthopus* species-group

E.9. *secretus* species-group

The tergal processes of this group consist of lateral tufted ring-shaped tubercles. The tubercles are located in an inconspicuous or a conspicuous depression. This kind of tubercles are short, evenly wide along their height, with a sharp rim, each with a tuft of setae on the top. The pits are usually wide, and the tufts do not cover the whole pit, so that the pits are easily observable.

Check list, four species:
cacirus Colombo & Azevedo, 2016
excellens Redighieri & Azevedo, 2006 from *incertae sedis*
secretus Colombo & Azevedo, 2016
puteolus Evans, 1969 from *incertae sedis*

E.10. *setosus* species-group

The tergal processes of this group consist of lateral tufted navel-shaped tubercles. Each tubercle is

located in a depression varying from inconspicuous to conspicuous. The lateral surface of metasomal tergite II has thick setae close to the depressions, which represent the main character of this group.
Many species of this group have a small body with inconspicuous tergal processes which have reduced tubercles, as in the Nearctic species *D. arizonicus* Evans, *D. barberi* Evans, *D. californicus* Ashmead, and *D. kansanus* Evans. However, some species with small bodies can have large tubercles, as the Neotropical *D. boiuna*.

Check list, 30 species:
areius Brito & Azevedo, 2017
aretisus Brito & Azevedo, 2017
arizonicus Evans, 1962 from *kansanus* species-group
barberi Evans, 1955 [1954] from *xanthopus* species-group
boibumba Colombo & Azevedo, 2018
boiuna Colombo & Azevedo, 2018 from *incertae sedis*
californicus Ashmead, 1893 *xanthopus* species-group
capelobo Colombo & Azevedo, 2018
caviclypeus Evans, 1969 from *incertae sedis*
citus Brito & Azevedo, 2017
crassus Redighieri & Azevedo, 2006
distans Redighieri & Azevedo, 2006
divisus Redighieri & Azevedo, 2006
filiformis Redighieri & Azevedo, 2006
firmus Redighieri & Azevedo, 2006
inflexus Redighieri & Azevedo, 2006
iracema Colombo & Azevedo, 2018
joaquinae Colombo & Azevedo, 2018
kansanus Evans, 1955 [1954] from *kansanus* species-group
magnus Redighieri & Azevedo, 2006 from *incertae sedis*
mapinguara Colombo & Azevedo, 2018 from *incertae sedis*
matintaperera Colombo & Azevedo, 2018 from *incertae sedis*
mirim Colombo & Azevedo, 2016 from *secretus* species-group
politus Ashmead, 1894 from *incertae sedis*
purius Colombo & Azevedo, 2016 from *incertae sedis*
sartus Brito & Azevedo, 2017
setosus Redighieri & Azevedo, 2006
spissus Redighieri & Azevedo, 2006
teobus Brito & Azevedo, 2017
w-aedeagus Colombo & Azevedo, 2016

E.11. *tuberculatus* species-group

The tergal processes of this group consist of sublateral or lateral tufted ring- or navel-shaped tubercles. Each tubercle is located in a depression, which can be inconspicuous or not. The tubercles and their tufts are slightly directed mesad (Azevedo, 2003). This kind of orientation is also present in some groups with median processes like *stellatus*, *basidentatus* and *vallensis*, but is unique among the *Dissomphalus* with lateral tergal processes.
The *strabus* species-group is here fused with the *tuberculatus* species-group. In the former group the tergal processes are slightly more sublateral, and this subtle variation does not justify a separate group as proposed by Azevedo (2003).

Check list, four species:
plaumanni Evans, 1964
strabus Azevedo, 2003 from *strabus* species-group
thysanus Azevedo, 2003 from *strabus* species-group
tuberculatus Ashmead, 1894

F. *Species known only from females*

The taxonomic position of the species known only from females remain unsolved. That is because the dimorphism is expressed in small blind apterous females and large macropterous males (Azevedo, 2003). Thus, only couples taken in phoretic copulation are able to be solved the problem of conspecific association (Azevedo *et al.,* 2016), or molecular tools.

Check list, 11 species:
attaphilus (Bruch, 1916)
azarai (Ogloblin, 1930)
catalinae Vargas & Terayama, 2002
claviger Evans, 1955 [1954]
crassicornis (Wasmann, 1899)
luscus Evans, 1964
mexicanus (Westwood, 1839)
platensis (Bruch, 1916)
scrupeus Evans, 1964
singularis Evans, 1962
yu Snelling, 1996

DISCUSSION

When I started working on *Dissomphalus* in the late 1990s, the genus had 52 Neotropical species and eight Nearctic species, five of them ranging also through Central America, as listed by Gordh & Móczár (1990). These numbers are nothing compared to the almost 300 valid New World species and the hundreds of undescribed ones I have seen throughout this time. Because of this hyper diversity, organizing *Dissomphalus* in species groups in order to facilitate its alpha taxonomy is crucial, and it has been a big challenge over the last 50 years.
The genitalia of *Dissomphalus* offer very useful characters to separate species because they vary immensely among species with clear morphological gaps, but with few intraspecific variations. On the other hand, at the species-group level, these gaps are sometimes not clear. Thus, in many cases, doubts can come up while utilizing the keys or even when studying the groups.

Except for the *napo* group, the new groups proposed here are partially (*chiapanus*) or fully (*lamellatus*, *rettenmeyeri*, *confusus*, *cornutus*, and *fungosus*) composed by species never allocated in any group before. These constitute the majority of the *incertae sedis* species in the genus in the Neotropical region, all of them having lateral processes. I established categories according to the shape of the processes in pitted, tufted and tubercled processes in order to accommodate the *incertae sedis* species in the groups. The latter was also subdivided according to the possession of navel-, ring- or callus-shaped tubercles. Thus, these groups differ from each another in details of the tergal process morphology, and because of that sometimes distinguishing groups is a hard task.

One example that illustrates this difficulty in group delimitation are the *conicus* and *setosus* species-groups, two large groups in numbers of species. They have the classical lateral navel-shaped tubercles in depressions, which vary from inconspicuous to conspicuous, or they can even be absent. Anyway, the surface lateral to the depressions or the corresponding area when without the depressions, have conspicuous and somewhat thick setae in *setosus* (Redighieri & Azevedo, 2006). These setae are few and delicate in *conicus* (Azevedo, 2003). Nonetheless, there are some species in the *conicus* group, whose setae are not so delicate, or in some species of the *setosus* group not so thick. This problem has already been raised by Colombo & Azevedo (2018), when indicating *D. matintaperera*, *D. mapinguari* and *D. caipora* as species which link both groups. Thus, in cases of doubt in couplet 35 of the keys, I recommend following both ways.

Problems of ambiguity can even occur between clusters of groups. In some instances, affirming that the tergal processes are median or lateral is hard. By definition, the tergal processes are considered median when located inside the median third of the tergal width, but sometimes the process can expand further than this limit. The tergal processes are considered lateral when located on the lateral thirds of the tergal width, but sometimes the processes are located exactly on the limit of the median and lateral tergal width. So, the position of the tergal processes when lateral can be more mesad or more laterad, but always not connected by a single median depression. The *cornutus* and *punctatus* species-groups are two examples in which the lateral tergal processes are located at the limit of the median and lateral tergal width (Azevedo 2003), and consequently are a matter of precaution at couplet 5 in the key. On the other hand, *brasiliensis* is an example of a species-group with median tergal processes (Redighieri & Azevedo, 2006), which needs precaution in the same couplet because it does have a single depression medially. Thus, the important tip to help understanding if the processes are median or lateral is to check if the species have single or double depressions.

Several new groups were created here to accommodate the huge diversity held in this genus. Nevertheless, I also fused several groups in order to avoid concept overlapping among them. That is the case in the *basidentatus*, *vallensis* and *stellatus* species-groups (Azevedo, 1999a). These groups were defined in a combination of characters that are always partially present in at least two of these three groups. Another case are the *strabus* and *tuberculatus* species-groups, defined by having tubercles slightly directed to each other (Azevedo, 2003). The only significant difference is the depth of the depression, which seems to me very little to justify splitting this group.

I also took this opportunity to improve or set up the definition of some groups. For instance, the original definition of the *secretus* species-group is inconsistent. It is based on four characters, such as metasomal tergum II with lateral depressions or not, 2) well-defined side pits, circular-shaped, higher edges, 3) tubercle below the surface of the tergite, many setae at the apex, and 4) bristles on the edge of the depressions or not (Colombo & Azevedo, 2018). The characters 1 and 4 are useless, because both conditions of presence and absence are possible, so that they do not help to understand the identity of the group. Anyway, when the depression has bristles, then the species belongs to the *setosus* species group, like for instance *D. mirim*. Character 2: 'well defined pit', refers to a wide pit located at the top of the tubercle. Thus, characters 2 and 3 have to be combined as: 'tubercle with pit at the top, from where a tuft of setae is raised'. This structure is quite common in the genus. And, because of that, it would run to the *conicus* species-group, except by the fact that in this latter group the tubercle is navel-shaped, whereas in the *secretus* group it is ring-shaped. However, it is not easy to distinguish navel and ring-shaped tubercles, because of their tiny size and range of variation. Therefore, we need precaution at couplet 37 in the key. As a result, the definition of this group was fully redesigned.

The species-group organization that I propose here is the first attempt to encompass all species, and I am sure that much is still necessary to improve the system and make the key more accurate. I am also conscious that there still are many undescribed species which can provoke instability in this group organization, because of two reasons. First, new species can be in the limit of two groups, and second, new groups can arise.

It is necessary to emphasize that the species-groups were conceived under an alpha taxonomic approach unlinked from a phylogenetic perspective. That is the justification of why I have utilized the word organization in the title instead of classification. I adopted this approach because of some reasons. First, a species-group is an informal rank and not subject to nomenclatural rules (ICZN, 1999). Second, the establishment of species-groups is supposed to be useful only to help people to identify species in this huge genus. Third, morphological and

molecular phylogenetic analyses of a genus with more than 400 species is time consuming, and the key for the species-group is urgent, otherwise species identification is a big hurdle.

Finally, I have seen more than 20 thousand unidentified specimens of Pan-American *Dissomphalus*, likely representing hundreds of new species. Certainly, there will be species that cannot be allocated to any species-group proposed here. Thus, I foresee the need for proposing in the future additional new species-groups in this speciose genus of flat wasps.

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REFERENCES

Alencar I.D.C.C., Azevedo C.O. 2006. Definition of Neotropical *coronatus* species-group (Hymenoptera: Bethylidae, *Dissomphalus*) with description of thirteen new species. *Zootaxa* 1330: 1-26. DOI: 10.11646/zootaxa.1330.1.1

Alencar I.D.C.C., Azevedo C.O. 2008. A new species-group of *Dissomphalus* (Hymenoptera: Bethylidae), with description of thirteen new species. *Zootaxa* 1851: 1-28. DOI: 10.11646/zootaxa.1851.1.1

Alencar I.D.C.C., Waichert C. & Azevedo C.O. 2018. Opening Pandora's box of Pristocerinae: molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethylidae) reveal several hidden genera. *Systematic Entomology* 43: 481-509. DOI: 10.1111/syen.12295

Ashmead W.H. 1893. A monograph of the North American Proctotrypidae. *Bulletin of the United States National Museum* 45: 1-472. DOI: 10.5479/si.03629236.45.1

Ashmead W.H. 1894. Report on the parasitic Cynipidae, part of the Braconidae, the Ichneumonidae, the Proctotrypidae, and part of the Chalcididae. Part III. *Journal of Linnean Society of London, Zoology* 25: 188-254.

Azevedo C.O. 1999a. Revision of the Neotropical *Dissomphalus* Ashmead, 1893 (Hymenoptera, Bethylidae) with median tergal process. *Arquivos de Zoologia* 35: 301-394. DOI: 10.11606/issn.2176-7793.v35i4p301-394

Azevedo C.O. 1999b. On Nearctic *Dissomphalus* (Hymenoptera, Bethylidae), with the description of two new species from Florida. *Iheringia, Série Zoológica* 87: 49-56.

Azevedo C.O. 1999c. Additional notes on Systematic of Neotropical *Dissomphalus* Ashmead (Hymenoptera, Bethylidae). *Revista Brasileira de Zoologia* 16: 921-949.

Azevedo C.O. 2000. The *dumosus* group of *Dissomphalus* (Hymenoptera, Bethylidae): definition and description of a new Amazonian species. *Boletim do Museu Paraense Emílio Goeldi* 16: 91-97.

Azevedo C.O. 2001. Systematics of the Neotropical *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) of the *bicavatus* group. *Revista Brasileira de Entomologia* 45: 173-205.

Azevedo C.O. 2003. Synopsis of the Neotropical *Dissomphalus* (Hymenoptera, Bethylidae). *Zootaxa* 338: 1-74. DOI: 10.11646/zootaxa.338.1.1

Azevedo C.O., Colombo W.D., Alencar I.D.C.C., Brito C.D. de, Waichert C. 2016. Couples in phoretic copulation, a tool for male-female association in highly dimorphic insects of the wasp genus *Dissomphalus* Ashmead (Hymenoptera: Bethylidae). *Zoologia* 33(6): e20160076. 7p. DOI: 10.1590/S1984-4689zool-20160076

Azevedo C.O., Alencar I.D.C.C., Colombo W.D. 2018a. Pairs in copulation of the highly dimorphic genus *Pristocera* Klug (Hymenoptera, Bethylidae) from Madagascar solve taxonomic problems of male-female associations. *Zootaxa* 4433: 1-49. DOI: 10.11646/zootaxa.4433.1.1

Azevedo C.O., Alencar I.D.C.C., Ramos M.S., Barbosa D.N., Colombo W.D., Vargas R. J.M., Lim J. 2018b. Global guide of the flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4489: 1-294. DOI: 10.11646/zootaxa.4489.1.1

Brito C.D., Azevedo C.O. 2017. Review of *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) from Panama, with key to the Central American species. *Zootaxa* 4335: 1-72. DOI: 10.11646/zootaxa.4335.1.1

Bruch C. 1916. Descripción de dos himenópteros mirmecófilos pertenecientes á los Bethylidae. *Physis* 2: 19-23.

Colombo W.D., Azevedo C.O. 2016. Review of *Dissomphalus* Ashmead, 1893 (Hymenoptera, Bethylidae) from Espírito Santo, Brazil, with description of twenty-one new species. *Zootaxa* 4143: 1-84. DOI: 10.11646/zootaxa.4143.1.1

Colombo W.D., Alencar I.D.C.C., Limeira-de-Oliveira F. & Azevedo C.O. 2018. New species and records of *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) from Cerrado, Caatinga and relicts of the Atlantic Forest from northeastern Brazil. *Zootaxa* 4462: 1-40. DOI: 10.11646/zootaxa.4462.1.1

Evans H.E. 1955 [1954]. The North American species of *Dissomphalus* (Hymenoptera, Bethylidae). *Proceedings of the Entomological Society of Washington* 56: 288-309.

Evans H.E. 1962. Further studies on the genus *Dissomphalus* in the United States, Mexico, and Greater Antilles (Hymenoptera, Bethylidae). *Proceedings of the Entomological Society of Washington* 64: 65-78.

Evans H.E. 1963. A revision of the *Apenesia* in the Americas (Hymenoptera, Bethylidae). *Bulletin of the Museum of Comparative Zoology* 130: 249-359.

Evans H.E. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology* 132: 1-222.

Evans H.E. 1966. Further studies on Neotropical Pristocerinae (Hymenoptera, Bethylidae). *Acta Hymenopterologica* 2: 99-117.

Evans H.E. 1969. The genera *Apenesia* and *Dissomphalus* in Argentina and Chile (Hymenoptera, Bethylidae). *Breviora* 311: 1-23.

Evans H.E. 1978. The Bethylidae of America North of Mexico. *Memoirs of the American Entomological Institute* 27: 1-332.

Evans H.E. 1979. The genus *Dissomphalus* in Northwestern South America (Hymenoptera: Bethylidae). *Proceedings of the Entomological Society of Washington* 81: 276-284.

Gordh G., Móczár L. 1990. A catalog of the world Bethylidae

(Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute* 46: 1-364.

ICZN International Commission on Zoological Nomenclature. 1999. International Code on Zoological Nomenclature. Published by International Trust for Zoological Nomenclature c/o The Natural History Museum, London, UK. Available online at http://iczn.org/iczn/index.jsp.

Kieffer J.J. 1904. Description de nouveaux Dryininae et Bethylinae du Musée Civique de Gênes. *Annali del Museo Civico di Storia Naturale di Genova* 41: 351-412.

Kieffer J.J. 1906 [1905]. Beschreibung neuer Proctotrypiden aus Nord- und Zentralamerika. *Berliner Entomologische Zeitschrift* 50: 237-290.

Kieffer J.J. 1908. Nouveaux proctotrypides et cynipides d'Amérique recueillis par M. Baker. *Annales de la Société Scientifique de Bruxelles* 32: 7-64.

Kieffer J.J. 1910a. Description de nouveaux microhyménoptères du Brésil. *Annales de la Société Entomologique de France* 78: 287-348.

Kieffer J.J. 1910b. Description de nouveaux Béthylides (Hymen). *Annales de la Société Entomologique de France* 79: 31-56.

Kieffer J.J. 1911. Nouveaux Béthylides et Dryinides exotiques du British Museum de Londres. *Annales de la Société Scientifique de Bruxelles* 35: 200-233.

Kieffer J.J. 1914a. Trois nouveaux Béthylides. *Bulletin de la Société Entomologique de France*, 1: 60-61.

Kieffer J.J. 1914b. Bethylidae. *Das Tierreich* 41: 228-595.

Lanes G.O., Kawada R., Azevedo C.O., Brothers D. 2020. Revisited morphology applied for Systematic of flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4752: 1-127. DOI: 10.11646/zootaxa.4752.1.1

Ogloblin A.A. 1930. Notes on Bethylidae with the description of two new species from Misiones. *Revista de la Sociedad Entomologica Argentina* 3: 15-27.

Redighieri E.S., Azevedo C.O. 2004. New species and notes on *Dissomphalus* (Hymenoptera, Bethylidae) from Estação Biológica de Santa Lúcia, Santa Teresa, ES, Brazil. *Iheringia, Série Zoológica* 94: 329-333. DOI: 10.1590/S0073-47212004000300018

Redighieri E.S., Azevedo C.O. 2006. Fauna de *Dissomphalus* Ashmead (Hymenoptera, Bethylidae) da Mata Atlântica Brasileira, com descrição de 23 espécies novas. *Revista Brasileira de Entomologia* 50: 297-334. DOI: 10.1590/S0085-56262006000300001

Snelling R.R. 1996. Systematic notes on some Bethylidae from the Virgin Islands and Puerto Rico (Hymenoptera: Chrysidoidea). *Memoirs of the Entomological Society of Washington* 17: 194-208.

Vargas R. J.M., Terayama M. 2002. Five new species of the subfamily Pristocerinae (Insecta, Hymenoptera, Bethylidae) from Colombia. *Biogeography* 4: 25-31.

Wasmann E. 1899. Die Psychischen Fähigkeiten der Ameisen. *Zoologica*,11: 1-133.

Westwood J.O. 1839. Monograph upon the hymenopterous genus *Scleroderma*. *Transactions of the Royal Entomological Society of London* 2: 164-172.

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A new cave-dwelling centipede species from Croatia (Chilopoda: Lithobiomorpha: Lithobiidae)

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Abstract: A new species of minute cave-dwelling centipedes, *Lithobius radjai* sp. nov., is described and illustrated based on specimens collected from a cave in Croatia (Balkan Peninsula). A detailed account of the morphology of specimens of both sexes is provided. Furthermore, a brief comparison with other morphologically similar species is presented, and the type locality of the new species is mapped.

Keywords: "*Monotarsobius*" - troglomorphic - endemic - Dinaric karst - Dalmatia - Balkan Peninsula.

INTRODUCTION

As the largest limestone region in Europe, the Dinaric karst is one of the world's richest hotspots of subterranean biodiversity, inhabited by more than 900 troglobitic species (Sket *et al.*, 2004). This extraordinary number of troglobites increases every year, mostly as a result of cooperation between biologists and speleologists (Simičević, 2017). A large number of these taxa show a high degree of endemism, some of them having been recorded only from a single cave, pit and/or mountain massif. Even today, two and a half centuries after the description of the famous cave olm *Proteus anguinus* Laurenti, 1768, nearly 330 years after its first find (Valvasor, 1689), and almost 190 years after the description of the first cave-adapted blind arthropod (*Leptodirus hochenwartii* Schmidt, 1832), there still are new "major" discoveries from the Dinarides. Such are, e.g. the recent discovery and description of the first troglobitic scorpion in Europe (Karaman, 2020), a new millipede family (Antić *et al.*, 2018), etc. "Large" troglobitic and stygobitic species in different animal groups are still being discovered from Dinaric subterranean habitats, while the number of tiny arthropods, like the new species described here, is even higher (e.g. Antić *et al.*, 2016; Akkari *et al.*, 2017; Bedek *et al.*, 2019a, b; Lukić *et al.*, 2018; Pavićević *et al.*, 2020; Stoev *et al.*, 2015; Švara *et al.*, 2015).

In this study, we describe a tiny new cave-dwelling species of *Lithobius* Leach, 1814 on the basis of specimens collected from the cave Velika Ćulumova Pećina on the Kijevo karst plateau (part of the central Dinarides, southern Croatia, Balkan Peninsula).

MATERIAL AND METHODS

The type series of the new species includes 10 specimens (five females, four males and one larva III; labeled as L1-L10). Each analysed specimen is preserved in a single labeled vial with 70% ethanol. The material is deposited in the collection of the Natural History Museum, Split, Croatia (NHMSC), and in the collection of the Institute of Zoology, University of Belgrade, Faculty of Biology, Serbia (IZB).

After preparation of temporary microscope slides with glycerin, photos of body parts and whole specimens were made with a Canon PowerShot A80 digital camera connected to a Carl Zeiss Axioscope 40 compound microscope, as well as with a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller attached to a Nikon SMZ 1270 binocular stereo microscope. For processing of the final images we used the Zerene Stacker software (for focal stacking) and Adobe Photoshop CS6. The drawings were created from photos using tracing paper and a computer monitor. The specimens were measured using a Carl Zeiss Stemi 2000-C dissecting stereomicroscope with an AxioCam MRc camera and integrated Axio Vs40 software packages. The distribution map was created using the blank simple map of Croatia (downloaded from

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the web site "d-maps.com") and Adobe Photoshop CS6. The terminology of external morphology used in the description follows Bonato *et al*. (2010). The developmental stage of the only collected larval specimen (IZB ChL027-L9) was identified using the proposition for larval stage separation given by Andersson (1979). The description of antennal sensilla follows the terminology recommended by Müller *et al*. (2011). Finally, we used the ChiloBase electronic database (Bonato *et al*., 2016) to make a list of European species of the "subgenus *Monotarsobius* Verhoeff, 1905" [see the recommendations for selected *Lithobius* subgenera given by Ganske *et al*. (2021)] for the purpose of comparison with other morphologically similar species.

Abbreviations following Eason (1964) are used in the text and in the tables: a = anterior, C = coxa, D = dorsal, F = femur, m = median, p = posterior, Pf = prefemur, T, TT = tergite, tergites, Ti = tibia, Tr = trochanter, V = ventral. Other abbreviations in the figures used to mark some of the morphological structures are explained directly in the figure legends.

TAXONOMY

Lithobius radjai Stojanović, Antić & Makarov, sp. nov.

Figs 1-4

Holotype: NHMSC L10; female; Croatia, Šibenik-Knin County, Municipality of Kijevo, the cave Velika Ćulumova Pećina, under stones in dark part of the cave, 43.98925°N, 16.37227°E, 451 m a.s.l.; 15.04.2006; leg. T. Rađa.

Paratypes: NHMSC; 1 male, 1 female (NHMSC L1 and L4); same data as for holotype. – IZB; 3 males, 3 females, 1 larva III (IZB ChL027-L3, -L6 and -L7; IZB ChL027-L2, -L5 and -L8; and IZB ChL027-L9, respectively); same data as for holotype.

Diagnosis: The new species is distinguished from its congeners by a unique combination of characters: the translucent cuticle of its whitish body; small size (ca 5-6 mm in adults); antennae composed of 20-22 articles; two partly depigmented ocelli in a horizontal line; Tömösváry's organ slightly smaller or equal to adjoining ocellus; 2+2 coxosternal teeth; porodonts moderately slender; no triangular projections on posterior angles of all tergites; tarsi of legs 1-13 undivided; 1-2 (usually 2) roundish coxal pores; female gonopods with 2+2 coniform spurs and a tridentate apical claw; male gonopods short, with one long seta; no sexual dimorphism in terminal legs; posterior accessory spines on penultimate and ultimate legs present, without anterior accessory spines.

Lithobius radjai sp. nov. can be clearly distinguished from morphologically similar European *Lithobius* species by the combination of characters presented in Table 1.

Etymology: The new species is named in honour of our friend and colleague Tonći Rađa (Split, Croatia), a well-known biospeleologist and the collector of the type material of the new species. The epithet, a name in the genitive case, is a patronym.

Description:

Measurements: Female holotype 4.8 mm long, ca 0.5 mm in widest part of the trunk. Body length of female paratypes (n = 4), male paratypes (n = 4), and larva III (n = 1): 4.7-6 mm, 4.9-5.3 mm and 2.4 mm, respectively.

Colouration (Figs 1C, 4C): Whitish, with pale yellowish, slightly sclerotized parts (cephalic capsule, forcipular coxosternite, tergites, leg claws and antennae), translucent over entire surface, especially on legs and trunk; possible slight discolouration after nearly 15 years in ethanol.

Antennae: - $^1/_5$-$^1/_4$ of body length in adults, and $^1/_3$ of body length in larval specimen; ca 2.5 times longer than cephalic capsule, narrowing distad (Figs 1C-D, 2A). Mostly 20-22 antennal articles in adults (in holotype 22+20), larva III with 14 articles in both antennae. Terminal article ca 2.5 times as long as broad (Fig. 2A). In female holotype total length of left and right antenna 1.3 mm and 1.1 mm. Length of the antennae in male paratypes 1.2-1.4 mm; in female paratypes 1.0-1.2 mm; in larva III specimen each antennae ca 0.9 mm. All antennal articles with numerous sensilla trichodea. Additionally, last antennal article with sensilla microtrichodea distally and with two long sensilla basiconica laterally, one each on opposite sides of article (present also in larva III) (Fig. 2B).

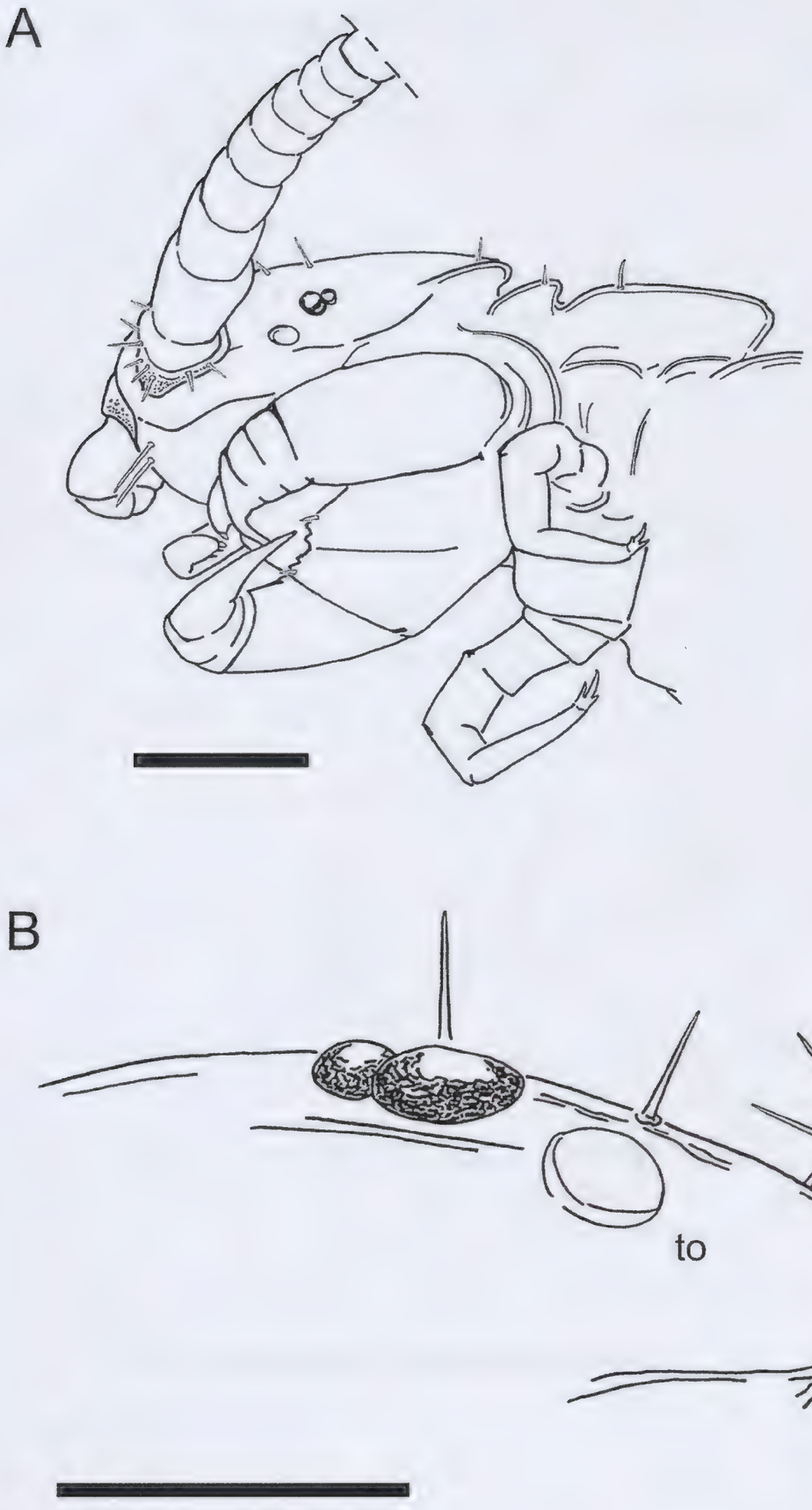
Cephalic plate: Generally smooth, with few setae mostly scattered on plate margin. Posterior margin almost straight; cephalic plate slightly narrowing anteriad (Fig. 2A). Plate length and width in holotype 0.47 mm and 0.49 mm, respectively; in male paratypes length 0.46-0.52 mm, width 0.45-0.51 mm; in female paratypes length 0.47-0.52 mm, width 0.47-0.51 mm; in larva III length 0.29 mm, width 0.34 mm (length/width ratio: holotype 0.96:1; male paratypes 1.02:1; female paratypes 1:1 to 1.04:1; larva III 0.85:1).

Ocelli: Two roundish ocelli on each side in a horizontal line (Fig. 1A-B); anterior ocellus almost twice as large as posterior one; both depigmented in the centre, with pale brown to chestnut brown pigmented ring around them.

Tömösváry's organ: Oval; slightly smaller or of same size as anterior ocellus; lying anteroventral to ocelli on anterolateral margin of cephalic capsule (Fig. 1A-B).

Forcipular segment (Fig. 2C): Coxosternite sub-trapezoidal; its anterior margin narrow, with external sides slightly higher than internal sides; dental margin with 2+2 small teeth of same size; medial diastema moderately deep, U-shaped, with approximately same width and depth; porodont moderately slender, positioned posterolateral to lateral tooth; no shoulders of forcipular coxosternite lateral to teeth; a few setae scattered in anterior part of coxosternite.

Tergites (Fig. 1C-D): All transparent, smooth; setae



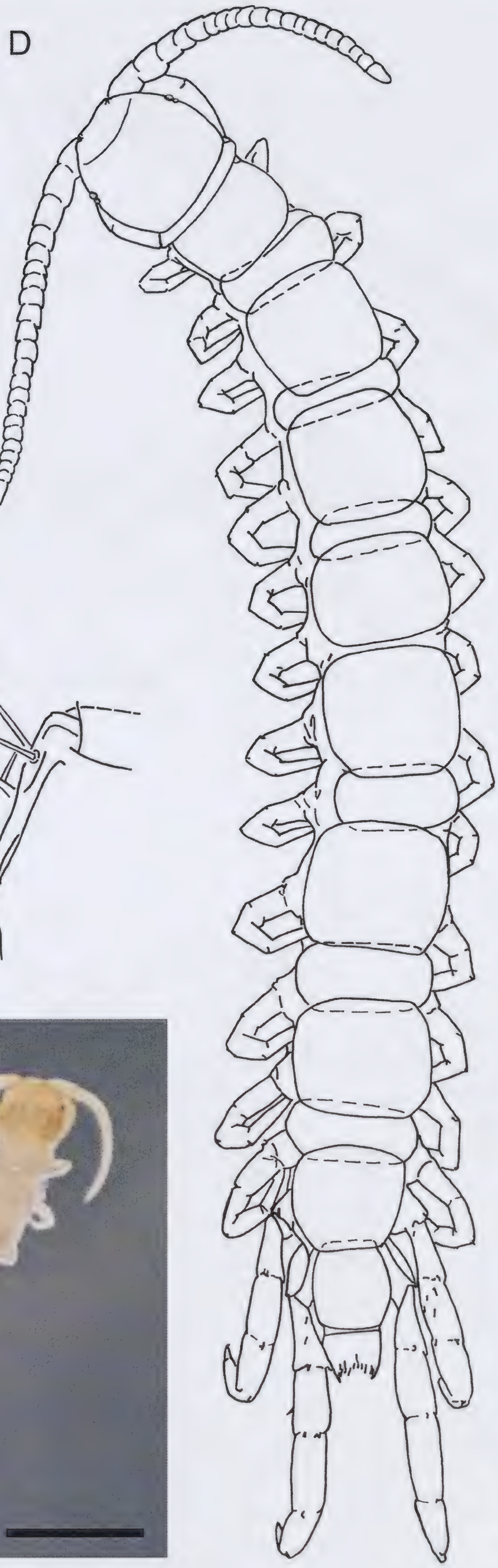


Fig. 1. *Lithobius radjai* sp. nov., ♀ paratype IZB ChL027-L5 (A), ♂ paratype IZB ChL027-L7 (B), ♀ holotype NHMSC L10 (C-D). (A) Head, ventrolateral view. (B) Ocelli and Tömösváry's organ on right side of cephalic capsule, ventrolateral view. (C) Habitus, dorsal view. (D) Habitus, dorsal view. Abbreviation: to = Tömösváry's organ. Scale bars: 1 mm (C-D); 0.5 mm (A); 0.1 mm (B).

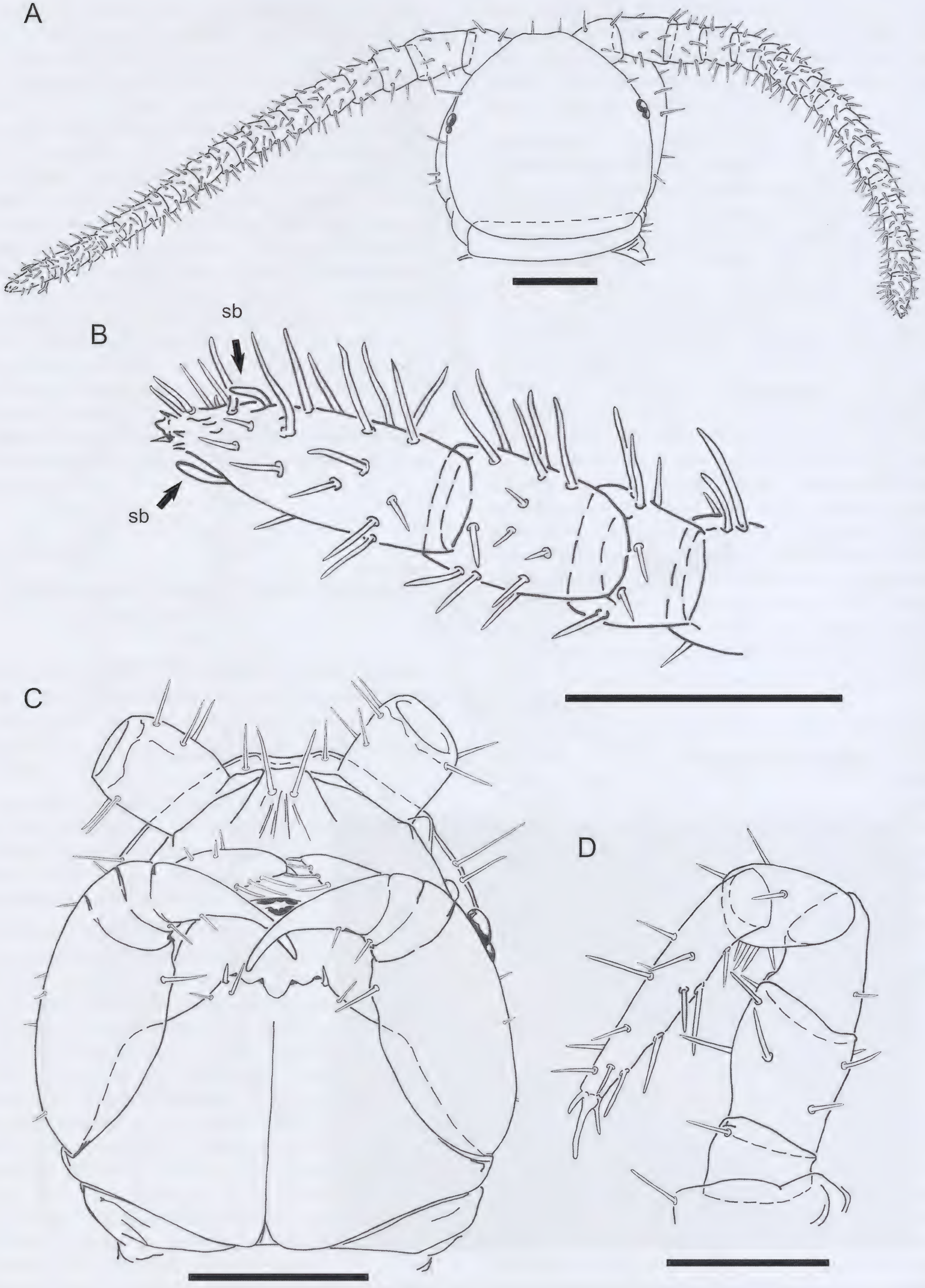


Fig. 2. *Lithobius radjai* sp. nov., ♀ holotype NHMSC L10 (A), larva III paratype IZB ChL027-L9 (B), ♂ paratype NHMSC L1 (C-D). (A) Head, dorsal view. (B) Distal part of right antenna, ventral view. (C) Head, ventral view. (D) Right leg 1, anteroventral view. Abbreviation: sb = sensilla basiconica. Scale bars: 0.2 mm (A, C); 0.1 mm (B, D).

Table 1. Comparison between *Lithobius radjai* sp. nov. and morphologically most similar species of European "*Monotarsobius*" [(?)* = type of accessory spines (anterior or posterior) on leg-pairs 14 and/or 15 not specified in species description].

Species	*Lithobius radjai* sp. nov.	*L. aeruginosus* L. Koch, 1862	*L. anacanthinus* (Matic, 1976)	*L. beshkovi* (Matic & Stavropoulos, 1988)	*L. biunguiculatus* Loksa, 1947
Body length (in mm)	4.7-6	6-11	5-6	9	6
Body colouration	whitish, translucent	orange-yellow	uniformly yellow	light brown	uniformly light yellow
Number of antennal articles	20-22	19-21	19-21	20	20
Cephalic plate length/width (ratio)	≈ 1:1	slightly longer than wide	1:1	1:1	wider than long
Ocelli	1-2 (in one row); partly depigmented	3-6 (usually in one row)	2 (in one row); black	2 (in one row); poorly visible	3-4 (in one row)
Tömösváry's organ	slightly smaller or of same size as terminal ocellus	of same size as terminal ocellus	significantly smaller than ocelli	significantly larger than ocelli	no data
Coxal pores	1-2 (usually 2)	2-4 (usually 3)	1-2 (usually 1)	2-3 (usually 2)	3-4
Plectrotaxy of 14th leg pair	V: -, m, m, m, -; D: -, -, p, -, -	V: -, m, amp, amp, -; D: a, -, mp, p, -	without spines	V: -, -; mp, m, -; D: -, -, mp, -, -	V: -, m, mp, m, -; D: -, -, mp, -, -
Plectrotaxy of 15th leg pair	V: -, m, m, m, -; D: -, -, p, -, -	V: -, m, amp, m, -; D: a, -, mp, p, -	without spines	V: -, -; mp, m, -; D: -, -, mp, -, -	V: -, m, mp, m, -; D: -, -, p, -, -
Accessory spines (anterior/posterior) of 14th leg pair	one (p)	absent	one (?)*	one (?)*	no data
Accessory spines (anterior/posterior) of 15th leg pair	one (p)	absent	one (?)*	absent	one (?)*
Gonopodal spurs (in female)	2+2	2+2	unknown	unknown	2+2
Number of gonopodal claws (in female)	3	3	unknown	unknown	3
Distribution	Croatia	widespread throughout Europe	Greece	Greece	Hungary, Poland, Romania, Slovakia
Habitat	Cave (troglobiont)	Epigeic; several records from caves (troglophile)	thermophilous forests; epigeic	caves and mesophilous forests	mesophilous forests; epigeic
Sources	this study	Loksa, 1947; Koch, 1862; Koren, 1992	Matic, 1976	Matic & Stavropoulos, 1988; Zapparoli, 1994, 2002	Loksa, 1947; Matic, 1966

scarce and irregularly scattered; posterior angles of all tergites rounded, without triangular projections; T1 rectangular in shape, with narrower posterolateral side; posterior margins of TT 1, 2, 4, 6, 8, 11 and 13 straight, in TT 5, 7, 9, 11 and 12 slightly convex, and in TT 3 and 10 slightly concave; anterior margin of TT 1, 5, 7, 8, 9, 11 and 13 straight, slightly convex in TT 3, 6, 10, 12 and 14, and slightly concave in TT 2 and 4; T9 widest of all tergites; intermediate tergites in both sexes with straight posterior margin.

Sternites: Smooth, translucent, with few setae mostly scattered on margins. Generally trapeziform, from more elongate (longer than wide in anterior part of the body) to more stockily trapezoidal (equal in length and width to wider than long in posterior part of body).

Legs: Moderately short and robust; their size progressively increasing toward posterior part, terminal legs noticeably larger than leg-pair 13 (Fig. 1D). Tarsi of legs 1-13 undivided (Fig. 2D). Tarsal articulation well defined in leg-pairs 14 and 15 (Figs 3A, C; 4A).

Table 1. (Continued)

Species	*L. dobrogicus* Matic, 1962a	*L. dudichi* Loksa, 1947	*L. hadzii* Matic & Dărăbanţu, 1968	*L. lagrecai* Matic, 1962b	*L. nudus* (Matic, 1976)
Body length (in mm)	5.5-7	8	4-5	3-3.5	3.5
Body colouration	yellowish	dark greenish brown	fawn yellowish	whitish	yellowish white
Number of antennal articles	20	19	20	19-20	17-18
Cephalic plate length/width (ratio)	≈ 1:1	wider than long	1:1	1:1	slightly longer than wide
Ocelli	4-6 (in 1-2 rows); clearly pigmented	6 (irregularly arranged)	5 (in 2 rows)	4 (in 2 rows); clearly pigmented	absent
Tömösváry's organ	same size as ocelli	almost twice as large as adjacent ocellus	same size as ocelli	smaller than largest ocellus	no data
Coxal pores	1-2 (usually 2)	1-3	1-2 (usually 2)	1-2 (usually 1)	1
Plectrotaxy of 14th leg pair	V: -, m, mp, m, -; D: -, -, mp, -, -	V: -, -, -, m, -; D: -, -, mp, -, -	V: -, m, amp, m, -; D: -, -, mp, -, -	V: -, -, m, m, m; D: -, -, p, -, -	without spines
Plectrotaxy of 15th leg pair	V: -, m, mp, m, -; D: -, -, mp, -, -	V: -, m, m, m, -; D: -, -, mp, -, -	V: -, m, amp, m, -; D: -, -, mp, -, -	V: -, -, (a)m, m, -; D: -, -, p, -, -	without spines
Accessory spines (anterior/posterior) of 14th leg pair	no data	both (a+p)	no data	both (a+p)	absent
Accessory spines (anterior/posterior) of 15th leg pair	absent	both (a+p)	one (?)*	absent	absent
Gonopodal spurs (in female)	2+2	unknown	unknown	unknown	unknown
Number of gonopodal claws (in female)	3	unknown	unknown	unknown	unknown
Distribution	Bulgaria, Romania	Poland, Romania	Croatia	Italy (Sicilia)	Greece
Habitat	epigeic	epigeic	epigeic	cave (presumed troglobiont)	epigeic; coniferous forest
Sources	Matic, 1962a, 1966	Loksa, 1947; Matic, 1966; Leśniewska *et al.*, 2015	Matic & Dărăbanţu, 1968	Matic, 1962b	Matic, 1976; Zapparoli, 2002

All legs with moderately long and curved claws. Long and slender anterior accessory spines present on claws of leg-pairs 1-13 (Fig. 2D). Anterior accessory spines absent on penultimate and ultimate legs. Posterior accessory claw present on all legs, relatively smaller on leg-pairs 14 and 15 (Fig. 3D-E). Glandular pores on inner side in penultimate and ultimate legs absent in both sexes. Plectrotaxy of female holotype and its variation in paratypes are summarized in Tables 2-8.

Coxal pore: Small, rounded, in a shallow gutter-like depression; poorly visible due to translucent cuticle of coxae; usually 2222, otherwise 1222 and 1221.

Male sexual characters (Fig. 3A-B): Sternite of ultimate leg-bearing segment trapeziform, with narrower posterior side; first genital sternite wider than long, with scattered short setae, posterior margin convex between the gonopods, without a medial bulge. Gonopods short, developed as small hemispheres, bulge-like, distally with a long seta. Penis moderately long, bilobed, with two long setae on each side. Telson wider than long, with several long setae on posterior margin. Leg-pairs 14 and 15 without any modifications.

Female sexual characters (Fig. 4): Ultimate sternite of same shape as in males; first genital sternite deeply concave in middle part of posterior margin between condyles of gonopods, with a well sclerotized small medial bulge within this incision. Gonopods: first gonopodal articles broad, each with 5-6 long setae on

Table 1. (Continued)

Species	*L. pasquinii* Matic, 1967	*L. paucispinus* (Matic, 1976)	*L. sivasiensis* (Matic, 1983)	*L. zveri* (Matic & Stentzer, 1977)
Body length (in mm)	5	6	7-9	3
Body colouration	yellowish white	fawn-yellow to fawn-brown	light yellow	whitish yellow
Number of antennal articles	20-21	20	20	20
Cephalic plate length/width (ratio)	no data	no data	≈ 1:1	≈ 1:1
Ocelli	1-2 (in one row); clearly pigmented	4 (in 2 rows); clearly pigmented	5 (in 2 rows); clearly pigmented	absent
Tömösváry's organ	more than twice as large as ocelli	smaller than ocelli	smaller than ocelli	extraordinarily large
Coxal pores	2	2	1-2	no data
Plectrotaxy of 14th leg pair	V: -, -, mp, m, m; D: -, -, mp, -, -	V: -, m, m, m, -; D: -, -, p, -, -	V: -, -, -, m, -; D: -, -, mp, -, -	V: -, -, m, m, -; D: -, -, p, -, -
Plectrotaxy of 15th leg pair	V: -, m, mp, m, -; D: -, -, mp, -, -	V: -, m, m, m, -; D: -, -, p, -, -	V: -, -, -, m, -; D: -, -, mp, -, -	V: -, -, m, m, -; D: -, -, p, -, -
Accessory spines (anterior/posterior) of 14th leg pair	one (?)*	one (?)*	one (?)*	one (?)*
Accessory spines (anterior/posterior) of 15th leg pair	absent	one (?)*	absent	one (?)*
Gonopodal spurs (in female)	unknown	unknown	2+2	unknown
Number of gonopodal claws (in female)	unknown	unknown	3	unknown
Distribution	Italy	Turkey	Turkey	Slovenia
Habitat	cave (presumed troglobiont)	epigeic	epigeic	cave (troglobiont)
Sources	Matic, 1967	Matic, 1976	Matic, 1983	Matic & Stentzer, 1977

ventral surface arranged in two rows and 1-2 moderately shorter dorsolateral setae; 2+2 sharp coniform spurs, inner spurs slightly smaller than outer ones; second gonopodal articles with 2-3 long ventral setae and 3-4 medium-short to long dorsolateral setae each; third articles with 2-3 medium-short to long dorsolateral setae; gonopodal claws moderately curved, tridentate, inner denticles smaller than outer ones, median and external denticles of approximately same size; without secondary sexual characters on penultimate and ultimate legs.

Type locality: The cave Velika Ćulumova Pećina, municipality of Kijevo, Šibenik-Knin County, Croatia (Fig. 5A).

Remarks: Jalžić (1974) described the cave Velika Ćulumova Pećina (its entrance shown in Fig. 5B-C) as one of the most beautiful speleological objects in all of Dalmatia, with approximately 360 m of tunnels. Located on the flattened Kijevo karst plateau in the municipality of Kijevo (Šibenik-Knin County, Croatia) (Fig. 5A), it is a well-known tourist attraction. Due to the presence of a reproductive colony of a protected bat species, this cave is protected by the "Natura 2000" ecological network (Natura code HR2000020) (Barišić, 2010). The cave is also known as the locality of *Alpioniscus* (*Illyrionethes*) *balthasari* (Frankenberger, 1937), an endemic Dinaric species of troglobitic trichoniscid woodlice (Bedek *et al.*, 2019b). The type material of *Lithobius radjai* sp. nov. was collected under stones in the dark part of the cave (Rađa, pers. comm.).

DISCUSSION

Due to the presence of more than 9000 registered caves and pits in Croatia, with some estimates that there are at least twice as many, the discovery of new species

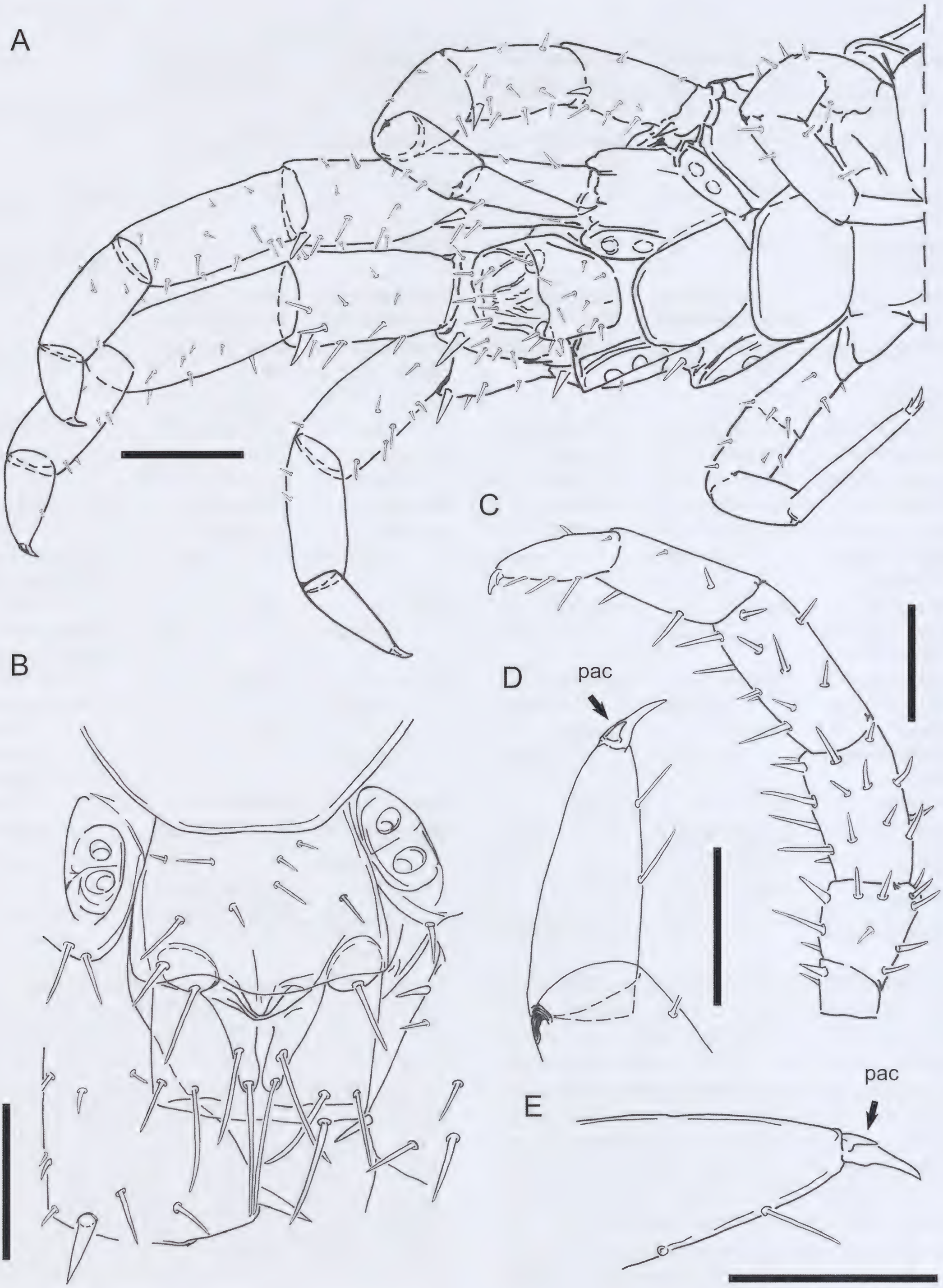


Fig. 3. *Lithobius radjai* sp. nov., ♂ paratype IZB ChL027-L3 (A), ♂ paratype NHMSC L1 (B, D-E), ♀ paratype NHMSC L4 (C). (A) Posterior part of body, ventrolateral view. (B) Posterior segments and gonopods, ventral view. (C) Right ultimate leg, posteroventral view. (D) Tarsus and pretarsus of right penultimate leg, posteroventral view. (E) Pretarsus of right ultimate leg, posteroventral view. Abbreviation: pac = posterior accessory claw. Scale bars: 0.2 mm (A, C); 0.1 mm (B, D-E).

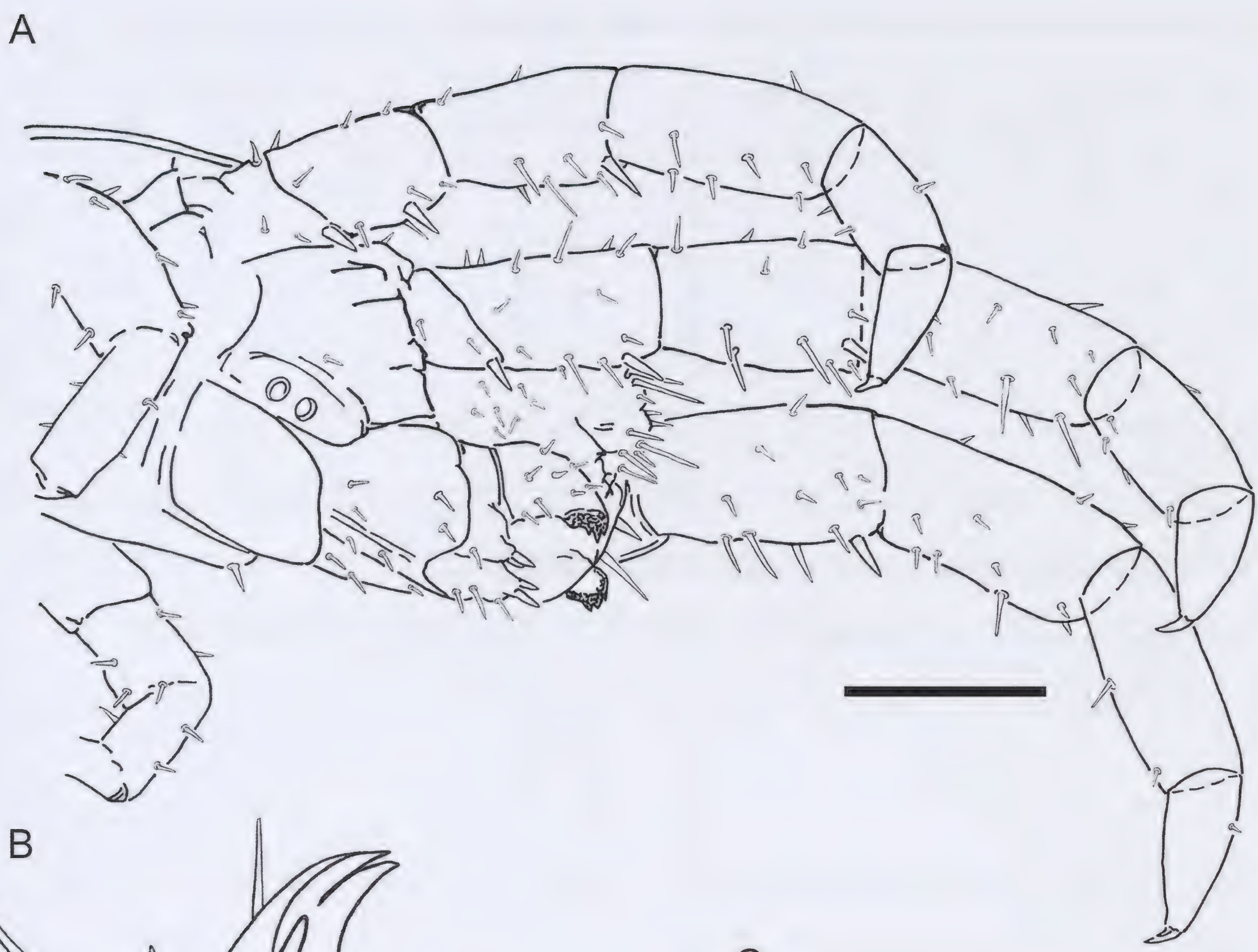


Fig. 4. *Lithobius radjai* sp. nov., ♀ paratype NHMSC L4 (A-B), ♀ holotype NHMSC L10 (C). (A) Posterior part of body, ventrolateral view. (B) Left gonopod, ventral view. (C) Gonopods, ventral view. Scale bars: 0.2 mm (A, C); 0.1 mm (B).

Table 2. Leg spinulation in *Lithobius radjai* sp. nov., female holotype (NHMSC L10).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1-3					m					a
4-5					m					ap
6				(m)	m					ap
7-9				m	m					ap
10				m	m					a(p)
11				m	m					a
12-13				m	m					
14-15		m	m	m				p		

Table 3. Leg spinulation in *Lithobius radjai* sp. nov., male paratype (NHMSC L1).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1					m					a(p)
2-3					m					ap
4-9				m	m					ap
10-11				m	m					a
12				m	m					
13			(m)	m	m					
14-15		m	m	m				p		

Table 4. Leg spinulation in *Lithobius radjai* sp. nov., female paratype (IZB ChL27 L2).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1					m					(a)
2					m					a
3				(m)	m					ap
4-11				m	m					ap
12				m	m					a(p)
13			m	m						a
14-15		m	m	m				p		

Table 5. Leg spinulation in *Lithobius radjai* sp. nov., male paratype (IZB ChL27 L3).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1-2					m					a
3				(m)	m					ap
4-11				m	m					ap
12-13				m	m					
14-15		m	m	m				p		

Table 6. Leg spinulation in *Lithobius radjai* sp. nov., female paratype (NHMSC L4), female paratype (IZB ChL27 L5) and male paratype (IZB ChL27 L7).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1-2					m					a
3				(m)	m					a(p)
4-9				m	m					ap
10-11				m	m					a
12-13				m	m					
14-15		m	m	m				p		

Table 7. Leg spinulation in *Lithobius radjai* sp. nov., male paratype (IZB ChL27 L6) and female paratype (IZB ChL27 L8).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1-2					m					a
3				(m)	m					ap
4-10				m	m					ap
11				m	m					a
12-13				m	m					
14-15		m	m	m				p		

Table 8. Leg spinulation in *Lithobius radjai* sp. nov., larva III (IZB ChL27 L9).

Legs	Ventral side					Dorsal side				
	C	Tr	Pf	F	Ti	C	Tr	Pf	F	Ti
1-4										
3-7					m					a
8					(m)					
9-10										

from subterranean habitats of this country is not a rare event (Jalžić *et al*., 2010). The majority of recorded subterranean species in Croatia are troglobionts, with 70% of them being endemic to Croatia (Gottstein Matočec *et al*., 2002). The last reported number of subterranean type localities in Croatia is 271, with a total of 427 animal species described from them (Jalžić *et al*., 2013), but this number increased in the decade after the publication of that paper. The present study adds one more endemic and presumed troglobitic species and one new type locality for Croatia (until now the cave Velika Ćulumova Pećina has not been reported as the type locality of any species). Based on several troglomorphic features such as the depigmented translucent cuticle due to its thinning (a common characteristic in cave species) (see Figs 1C and 4C), a reduced number of partly depigmented ocelli (Fig. 1B), as well as the fact that it is known only from the dark parts of the cave, at places with high humidity (under stones), we consider *Lithobius radjai* sp. nov. to be a troglobiont.

In light of a large number of morphological characters and existing sets of differing molecular data (both nuclear and mitochondrial markers), a recent study of Lithobiidae phylogeny conspicuously demonstrated the problematic taxonomic status of the subgenera *Monotarsobius*, *Lithobius* Leach, 1814 and *Sigibius* Chamberlin, 1913 (Ganske *et al*., 2021). The polyphyly of these subgenera was proven in that publication, and it was proposed to avoid using them in taxonomical studies. In other words, the diagnostic features of these *Lithobius* subgenera are results of homoplasy.

The new species presented here could be classified in the subgenus "*Monotarsobius*" on the basis of morphology.

Regardless of the validity and status of this subgenus, the congeners most similar to *Lithobius radjai* sp. nov. should be sought among species previously described under "*Monotarsobius*". The diagnostic characters common for all these species are: small size, usually short antennae with around 20 articles, coxosternite with 2+2 forcipular teeth, no posterior triangular projections on tergites, and undivided tarsi in leg-pairs 1-12(13) (summarized in Voigtländer *et al.*, 2017). In total, there are ca 120 species with such features, generally with a Palaearctic distribution (35 species in Europe and more than 80 in Asia (data extracted from Bonato *et al.*,

Fig. 5. Type locality of *Lithobius radjai* sp. nov. (A) Position on the map of Croatia. (B-C) Entrance to the cave Velika Ćulumova Pećina (photos by T. Rađa).

2016). For the purpose of this paper, the new species is compared with all European "*Monotarsobius*" species, and a detailed comparison with the 13 most similar ones from southeastern Europe, the Apennine Peninsula and western Turkey is provided.

Lithobius radjai sp. nov. shares many similarities with the compared species, but there are also certain differences to each of them. Unquestionably, the most interesting for comparison are species from the Dinarides, viz., *L. hadzii* Matic & Dărăbanţu, 1968 (an epigeic species endemic to Croatia) and *L. zveri* Matic & Stentzer, 1977 (a subterranean species endemic to Slovenia). For a detailed comparison with these two and other similar species, see Table 1.

Finally, one of the significant problems existing in *Lithobius* taxonomy is visible in Table 1. The descriptions of a large number of *Lithobius* species are incomplete and/or imprecise in treating some morphological structures of more or less strong taxonomical importance, and sometimes it is even the case that those characters are not included at all. All the mentioned shortcomings have resulted in inadequate descriptions of many taxa today, which leads to many problems in identification and comparison. Fortunately for the present study, this is not so much the case in the descriptions of most European "*Monotarsobius*" species. There are certain inaccuracies in the descriptions of the species included here that affect their comparability, but these mostly concern characters that are currently not recognized as taxonomically very important. For example, statements on the presence or absence of one or both accessory spines on the penultimate and the ultimate legs are often missing. Furthermore, even when it is provided, in cases where only one accessory spine is present, there is no specification as to whether it is an anterior or a posterior spine (summarized in Table 1). Similar examples, often dealing with much more significant morphological characters (such as the number of antennal articles, the number and/or arrangement of ocelli, the presence of coxosternal teeth and porodonts, features of the genital apparatus, plectrotaxy, etc.), point to the need for a detailed redescription of a significant percentage of *Lithobius* species.

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REFERENCES

Akkari N., Komerički A., Weigand A.M., Edgecombe G.D., Stoev P. 2017. A new cave centipede from Croatia, *Eupolybothrus liburnicus* sp. n., with notes on the subgenus *Schizopolybothrus* Verhoeff, 1934 (Chilopoda, Lithobiomorpha, Lithobiidae). *ZooKeys* 687: 11-43.

Andersson G. 1979. Taxonomical studies on the post-embryonic development in *Lithobius*, with a brief comparison with *Lamyctes* (Chilopoda: Lithobiomorpha). *Dissertation, University of Gothenburg, Gothenburg, Sweden*, 49 pp.

Antić D.Ž., Dražina T., Rađa T., Lučić L.R., Makarov S.E. 2016. Taxonomic status of the family Biokoviellidae Mršić, 1992 (Diplopoda, Chordeumatida): reconsideration, with a description of one new species. *European Journal of Taxonomy* 205: 1-23.

Antić D.Ž., Rađa T., Makarov S.E. 2018. Dalmatosomatidae, a new monotypic family, and *Dalmatosoma agaricum* gen. et sp. nov. (Diplopoda: Chordeumatida: Craspedosomatidea) from Croatia, Balkan Peninsula. *Zootaxa* 4403(2): 289-306.

Barišić T. 2010. Speleological research Natura 2000 in County of Šibenik-Knin in 2009 (pp. 1-11). *In*: Buzjak N., Paar D. (eds). Stručni Seminar o Zaštiti Spilja i Podzemne Faune, Ogulin, Croatia. *Zbornik Radova*, 85 pp.

Bedek J., Gottstein S., Taiti S. 2019a. Taxonomy of *Alpioniscus* (*Illyrionethes*): *A. magnus* and three new species from the Dinaric Karst (Isopoda: Oniscidea: Trichoniscidae). *Zootaxa* 4657(3): 483-502.

Bedek J., Taiti S., Bilaldžija H., Ristori E., Baratti M. 2019b. Molecular and taxonomic analyses in troglobiotic *Alpioniscus* (*Illyrionethes*) species from the Dinaric Karst (Isopoda: Trichoniscidae). *Zoological Journal of the Linnean Society* 187(3): 539-584.

Bonato L., Edgecombe G.D., Lewis J.G.E., Minelli A., Pereira L.A., Shelley R.M., Zapparoli M. 2010. A common terminology for the external anatomy of centipedes (Chilopoda). *ZooKeys* 69: 17-51.

Bonato L., Chagas-Jr A., Edgecombe G.D., Lewis J.G.E., Minelli A., Pereira L.A., Shelley R.M., Stoev P., Zapparoli M. 2016. ChiloBase 2.0 - A world catalogue of centipedes (Chilopoda). Available at: http://chilobase.biologia.unipd.it (accessed in May 2021).

Chamberlin R.V. 1913. The lithobiid genera *Nampabius*, *Garibius*, *Tidabius* and *Sigibius*. *Bulletin of the Museum of Comparative Zoology* 57(2): 37-104.

Eason E.H. 1964. Centipedes of the British Isles. *Frederick Warne, London*, 294 pp.

Frankenberger Z. 1937. Über eine neue *Illyrionethes* Art aus Dalmatien. *Zoologischer Anzeiger* 120: 173-176.

Ganske A.S., Vahtera V., Dányi L., Edgecombe G.D., Akkari N. 2021. Phylogeny of Lithobiidae Newport, 1844, with emphasis on the megadiverse genus *Lithobius* Leach, 1814 (Myriapoda, Chilopoda). *Cladistics* 37: 162-184.

Gottstein Matočec S., Ozimec R., Jalžić B., Kerovec M., Bakran-Petricioli T. 2002. Raznolikost i ugroženost podzemne faune Hrvatske [Diversity and vulnerability of groundwater wildlife of Croatia]. *Ministry of Environment and Physical Planning, Republic of Croatia, Zagreb, Croatia*, 82 pp.

Jalžić B. 1974. Ćulumova pećina u Dalmacija [The Ćulumova pećina Cave in Dalmatia]. *Naše Planine* 5-6: 104-105.

Jalžić B., Bedek J., Bilaldžija H., Cvitanović H., Dražina T., Gottstein S., Kljaković-Gašpić F., Lukić M., Ozimec R., Pavlek M., Slapnik R., Štamol V. 2010. Atlas špiljskih tipskih lokaliteta faune Republike Hrvatske, Svezak 1 [The cave type localities atlas of Croatian fauna, volume 1]. *Croatian Biospeleological Society, Zagreb, Croatia*, 261 pp.

Jalžić B., Bedek J., Bilaldžija H., Bregović P., Cvitanović H., Čuković T., Ćuković A., Dražina T., Đud L., Gottstein S., Hmura D., Kljaković-Gašpić F., Komerički A., Kutleša P., Lukić M., Malenica M., Miculinić K., Ozimec R., Pavlek M., Raguž N., Slapnik R., Štamol V. 2013. Atlas špiljskih tipskih lokaliteta faune Republike Hrvatske, Svezak 2 [The cave type localities atlas of Croatian fauna, volume 2]. *Croatian Biospeleological Society, Zagreb, Croatia*, 261 pp.

Karaman I. 2020. A new *Euscorpius* species (Scorpiones: Euscorpiidae) from a Dinaric cave - the first record of troglobite scorpion in European fauna. *Biologia Serbica* 42(1): 14-31.

Koch L. 1862. Die Myriapodengattung *Lithobius*. *J. L. Lotzbeck, Nürnberg*, 94 pp.

Koren A. 1992. Die Chilopoden-Fauna von Kärnten und Osttirol. 2. Lithobiomorpha. *Carinthia II* 52: 1-138.

Laurenti J.N. 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium Austriacorum. Genus *Proteus* (pp. 35-36). *Joan. Thom. de Trattnern, Viennae*, 214 pp.

Leach W.E. 1814. Crustaceology (pp. 383-437). *In*: Brewster D. (ed.), The Edinburgh Encyclopaedia, 7(2). *Balfour, Edinburgh,* 767 pp.

Leśniewska M., Jastrzębski P., Stańska M., Hajdamowicz I. 2015. Centipede (Chilopoda) richness and diversity in the Bug River valley (Eastern Poland). *In*: Tuf I.H., Tajovský K. (eds), Proceedings of the 16th International Congress of Myriapodology, Olomouc, Czech Republic. *ZooKeys* 510: 125-139.

Loksa I. 1947. Beiträge zur Kenntnis der Steinläufer-, Lithobiiden-Fauna des Karpatenbeckens. I. *Fragmenta Faunistica Hungarica* 10(3): 73-85.

Lukić M., Delić T., Zagmajster M., Deharveng L. 2018. Setting a morphological framework for the genus *Verhoeffiella* (Collembola, Entomobryidae) for describing new troglomorphic species from the Dinaric karst (Western Balkans). *Invertebrate Systematics* 32(5): 1118-1170.

Matic Z. 1962a. Noi contribuţii la cunoaşterea subgenului *Monotarsobius* Verh. (*Chilopoda-Lithobius*) din fauna Republicii Populare Romîne. *Studii şi Cercetări de Biologie (Cluj)* 13(1): 75-86.

Matic Z. 1962b. Beiträge zur Kenntnis der Chilopoda aus Sizilien. *Bollettino delle Sedute dell'Accademia Gioenia di Scienze Naturali in Catania* (Serie 4) 7(2): 51-62.

Matic Z. 1966. Fauna Republicii Socialiste România. Clasa Chilopoda, Subclasa Anamorpha. Volumul VI, Fascicula 1. *Acadmia Republicii Socialiste România, Bucureşti, România*, 267 pp.

Matic Z. 1967. Contribution à la connaissance des Lithobiides, Scutigérides et Cryptopsides des grottes de l'Italie (Myriopoda). *Fragmenta Entomologica* 5(1): 77-110.

Matic Z. 1976. Sur quelques Myriapodes Chilopodes du Muséum d'Histoire naturelle de Genève. *Revue suisse de Zoologie* 83(2): 287-306.

Matic Z. 1983. Litobidi raccolti in Turchia dal Dott. Giuseppe Osella (Chilopoda Lithobiomorpha). *Fragmenta Entomologica* 17(1): 19-45.

Matic Z., Dărăbanţu C. 1968. Contributions à la connaissance des chilopodes de Yougoslavie. *Academia Scientiarum et Artium Slovenica. Classis IV. Historia Naturalis et Medicina. Pars Historiconaturalis* 11(5): 201-227.

Matic Z., Stavropoulos G. 1988. Contributions à la connaissance des chilopodes de Grèce. *Biologia Gallo-Hellenica* 14(1): 33-46.

Matic Z., Stentzer I. 1977. Beitrag zur Kenntnis der Hundertfüssler (Chilopoda) aus Slowenien. *Biološki Vestnik* 25(1): 55-62.

Müller C.H.G., Sombke A., Hilken G., Rosenberg J. 2011. Chilopoda - Sense organs (pp. 235-278). *In*: Minelli A. (ed.), Treatise on zoology - Anatomy, taxonomy, biology. The Myriapoda. Volume 1. *Brill, Leiden*, 530 pp.

Pavićević D., Lohaj R., Popović M. 2020. A new genus and species of subterranean trechine beetle from Montenegro (Coleoptera: Carabidae: Trechini). *Biologia Serbica* 42(1): 48-59.

Schmidt F. 1832. Beitrag zu Krain's Fauna. *Leptodirus Hochenwartii*, n. g., n. sp. *Illyrisches Blatt, Laibach* 3: 9-10.

Simičević V. 2017. Poachers threaten Balkans' underground biodiversity. *Science* 358(6367): 1116-1117.

Sket B., Paragamian K., Trontelj P. 2004. A census of the obligate subterranean fauna in the Balkan Peninsula (pp. 309-322). *In*: Griffiths H.I., Krystufek B., Reed, J.M. (eds), Balkan biodiversity. Pattern and process in Europe's biodiversity hotspot. *Kluwer Academic Publishers, Dordrecht*, 358 pp.

Stoev P., Akkari N., Komerički A., Edgecombe G.D., Bonato L. 2015. At the end of the rope: *Geophilus hadesi* sp. n. - the world's deepest cave-dwelling centipede (Chilopoda, Geophilomorpha, Geophilidae). *In*: Tuf I.H., Tajovský K. (eds), Proceedings of the 16th International Congress of Myriapodology, Olomouc, Czech Republic. *ZooKeys* 510: 95-114.

Švara V., Delić T., Rađa T., Fišer C. 2015. Molecular phylogeny of *Niphargus boskovici* (Crustacea: Amphipoda) reveals a new species from epikarst. *Zootaxa* 3994(3): 354-376.

Valvasor J.W. 1689. Die Ehre des Herzogthums Crain. *W.M. Endtner, Nürnberg*, 3532 pp.

Verhoeff K.W. 1905. Über die Entwicklungsstufen der Steinläufer, Lithobiiden und Beiträge zur Kenntnis der Chilopoden. *Zoologische Jahrbücher, Abteilung für Systematik* 8: 195-298.

Voigtländer K., Iorio E., Decker P., Spelda J. 2017. The subgenus *Monotarsobius* in the Iberian Peninsula with a description of a new pseudo-cryptic species from Northern Spain revealed by an integrative revision of *Lithobius crassipes* L. Koch, 1862 (Chilopoda, Lithobiomorpha, Lithobiidae). *ZooKeys* 681: 1-38.

Zapparoli M. 1994. Note tassonomiche e faunistiche su chilopodi della Grecia (Chilopoda). *Fragmenta Entomologica* 26(1): 11-66.

Zapparoli M. 2002. A catalogue of the centipedes from Greece (Chilopoda). *Fragmenta Entomologica* 34(1): 1-146.

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Morphological and morphometric variability in *Pergamasus decebali* and *P. scorilai* (Acari: Parasitidae), with comments on other species of the *P. crassipes* species-group

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Abstract: Intra- and interspecific variability of *Pergamasus scorilai* Juvara-Balş, 1973 and *P. decebali* Juvara-Balş, 1973 from Romania is investigated through morphological comparison and morphometric analyses. An analysis of morphological differences is used to show intraspecific variability and to establish the taxonomic limits of each species. We studied the proximal apophysis of tibia II in males and the endogynium of females. Using multivariate analyses based on 10 and 9 measurements for males and females, respectively, we demonstrate that the two species can be distinguished unambiguously. Relying on a variable selection approach, we also determine the most useful characters for the identification of these two very similar species. In this case only two tibial measurements allowed to correctly identify all male individuals, while at least six different measurements are needed for the discrimination of female specimens. Finally, we provide an exhaustive overview of male characteristics for the entire species-group, and we place *P. instipatus* Athias-Henriot, 1967 in the synonymy of *P. caninatellus* Athias-Henriot, 1967.

Keywords: Gamasid mites - species recognition - discriminant analysis - Romania.

INTRODUCTION

The genus *Pergamasus* Berlese, 1903 is one of the most common predatory mites in leaf litter and soil in the Northern Hemisphere. The genus was considered by Berlese (1903) as a subgenus of *Gamasus* Latreille, 1802 and raised by Hull (1918) to the generic level. The taxonomy of the genus was studied and revised by several authors (Bhattacharyya, 1963; Schweizer, 1961; Micherdzinski, 1969; Athias-Henriot, 1967, 1971). The classification established by Athias-Henriot (1971) is the one currently recognized (Juvara-Balş, 1976; Karg, 1993; Hrúzová & Fend'a, 2018). Athias-Henriot (1971) split *Pergamasus* s. lat. into three subgenera: *Thenargamasus*, *Triadogamasus* and *Pergamasus* s. str. The species included in *Pergamasus* s. str. are currently divided into four species-groups: the *crassipes*-group, the *beklemischevi*-group, the *alpinus*-group and the *athiasae*-group (Athias-Henriot, 1968; Juvara-Balş, 1970). The identification of species in the *Pergamasus crassipes* species-group, especially *P. crassipes* (Linnaeus, 1758), is difficult because of the lack of information on the variability of the main characteristics and because of incomplete descriptions. Micherdzinski (1969) enumerated all localities in Europe from where true *P. crassipes* were identified and pointed out that a revision was necessary because the occurrence of a complex of multiple species could not be excluded. *Pergamasus crassipes* and *P. longicornis* Berlese, 1906 were the first species to be assigned to the *crassipes* group (Bhattacharyya, 1963). Athias-Henriot (1967) subsequently added seven additional species and Juvara-Balş (1970, 1973) another six species from Romania. Karg (1993) only included six taxa of this species-group from central Europe in his identification key. He also considered *P. crassipes* and *P. longicornis* to belong to the same species with a great variability in the shape of the endogynium (Karg, 1993: fig. 315). Dielmann (1991) drew attention to the importance of better taxonomic descriptions of females but did not propose an updated diagnosis to separate the females of the different species. Considerable morphological variability within the *Pergamasus crassipes* species-group is regarded by some acarologists as mainly intraspecific (Karg, 1993), whereas others (Bhattacharyya, 1963; Athias-Henriot, 1967; Juvara-Balş, 1976) think that it warrants the separation of additional species. This confusing situation still prevails because the species-group has recently received little attention. In many ecological and biodiversity studies species identification is restricted to "*Pergamasus* sp.". This led us to investigate the level of variation between and within two closely related species, i.e. *P. scorilai*

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and *P. decebali*. These two species are morphologically similar to one another, although well-differentiated from the other species of the *P. crassipes* species-group in Romania (Juvara-Balş, 1976). Their identification based on discrete characters is difficult, and we wanted to assess whether morphometrics could provide an effective tool for species differentiation.

Collecting was conducted in the southern and western Carpathian Mountains of Romania where several populations of both species can be found in forest soils. Based on a sample of 257 individuals we assess and describe the variability of morphological and morphometric characters in *P. scorilai* and *P. decebali* to determine if it can be attributed to intraspecific polymorphism or to the presence of an overlooked species diversity.

MATERIAL AND METHODS

Morphological analyses

Two populations of *Pergamasus scorilai* and one of *P. decebali* were selected for morphological and morphometric analyses. The mites were collected by sifting leaf litter from two forests in western Romania, from the surface area of about one square meter each. Only adult individuals were used for the analyses. The specimens examined are:

- *P. decebali* (type series): 41 males, 31 females; spruce litter, Scarisoara Village, Apuseni Mountains, Alba County, 1100 m a.s.l.; 26.AUG.1970; leg. I. Juvara-Balş.
- *P. scorilai* (type series): 48 males, 47 females; beech forest, Sucu Valley, Maru Village, Caras-Severin County, 600 m a.s.l.; 29.SEP.1970; leg. I. Juvara-Balş.
- *P. scorilai*: 45 males, 45 females; spruce forest, Mount Mic, Caras-Severin County, 1800 m a.s.l.; 1.OCT.1970; leg. I. Juvara-Balş.

The holotypes and other specimens were deposited in the Emil Racovitza Institute of Speleology of the Romanian Academy, Bucarest, Romania. Four female *P. decebali* specimens, and one male and two female *P. scorilai* specimens from Mount Mic were deposited in the Natural History Museum of Geneva, Switzerland. All mites were cleared in lactic acid, and measurements were taken from dissected and slide-mounted specimens. Identification of species requires a special examination of males, which possess more distinct diagnostic characters than females. It is important to keep tibia II in a horizontal position (Fig. 1D) to observe the morphological characteristics and take measurements as established by Athias-Henriot (1967). The three following measurements were taken from both sexes: LI - length of idiosoma; t1 - length of tarsus I (Fig. 1C); t4 - length of tarsus IV. In males we additionally measured: AB - length of tibia II; AC - length of proximal apophysis of tibia II; GH - distance between base of distal apophysis and distal tibial margin; EF - distance between insertion of seta al1 and distal tibial margin; al1, al2 and pv1 - length of al1, al2 and pv1 setae, respectively, from insertion to tip (Fig. 1D). Finally, we selected the following morphometric characters in order to differentiate the females: LE - length of epigynium measured along its midline; WEB - width of posterior margin of epigynium; LSS - length of sternal shield; WSS - width of sternal shield (measured at the st2 setae level); W/2 - length of right half of posterior sternal margin; st5-st5 - distance between the insertions of the pair of setae st5 (Fig. 1A-B). All the measurements are in micrometres. All individual measurements are available online as Supplementary Material (https://doi.org/10.5281/zenodo.5082959). In addition to these standard measurements, we calculated two new variables: t1/LI - ratio between length of tarsus I and length of idiosoma; t4/LI - ratio between length of tarsus IV and length of idiosoma. The latter two variables were not included in most analyses, but were only used to compare the relative length of limbs in each of the three populations, in order to determine their correlation with the altitude as postulated by "Allen's rule" (Ray, 1960; Bidau & Martí, 2008).

The nomenclature of different structures of the endogynium follows Athias-Henriot (1967). The endogynium comprises a sack which has ventrally a pair of reticulated sphaerules that are separated by the stipula ("endogynial process" according to some authors) and are flanked by a pair of trabeculae. In species where these structures are variable (*P. crassipes*, *P. pinguicrus* Athias-Henriot, 1967, *P. scorilai*, *P. decebali*, *P. buerebistai* Juvara-Balş, 1973), identification based on the examination of a large series of specimens is advised.

Statistical analyses

First, a quick analysis of the morphometric male characters for all species of the *Pergamasus crassipes* species-group was done. This analysis allowed us to validate the reliability of these characters for species discrimination, and to identify where the two studied species (*P. decebali* and *P. scorilai*) lie among other members of the species-group. To this end we aggregated measurements used in Athias-Henriot (1967) and Juvara-Balş (1970, 1973) for all 15 species currently known in the *crassipes* species-group. We then carried out a principal component analysis (PCA) using the package ade4 (Dray & Dufour, 2007) available in the R environment (R Core Team, 2020).

For *P. decebali* and *P. scorilai*, both sexes were analysed separately and all analyses were conducted in R (R Core Team, 2020). Normality of data was tested using Shapiro tests. Means, standard deviation and coefficient of variability were calculated for each of the measured characters. Differences in mean measurements were assessed between *P. scorilai* and *P. decebali*, and

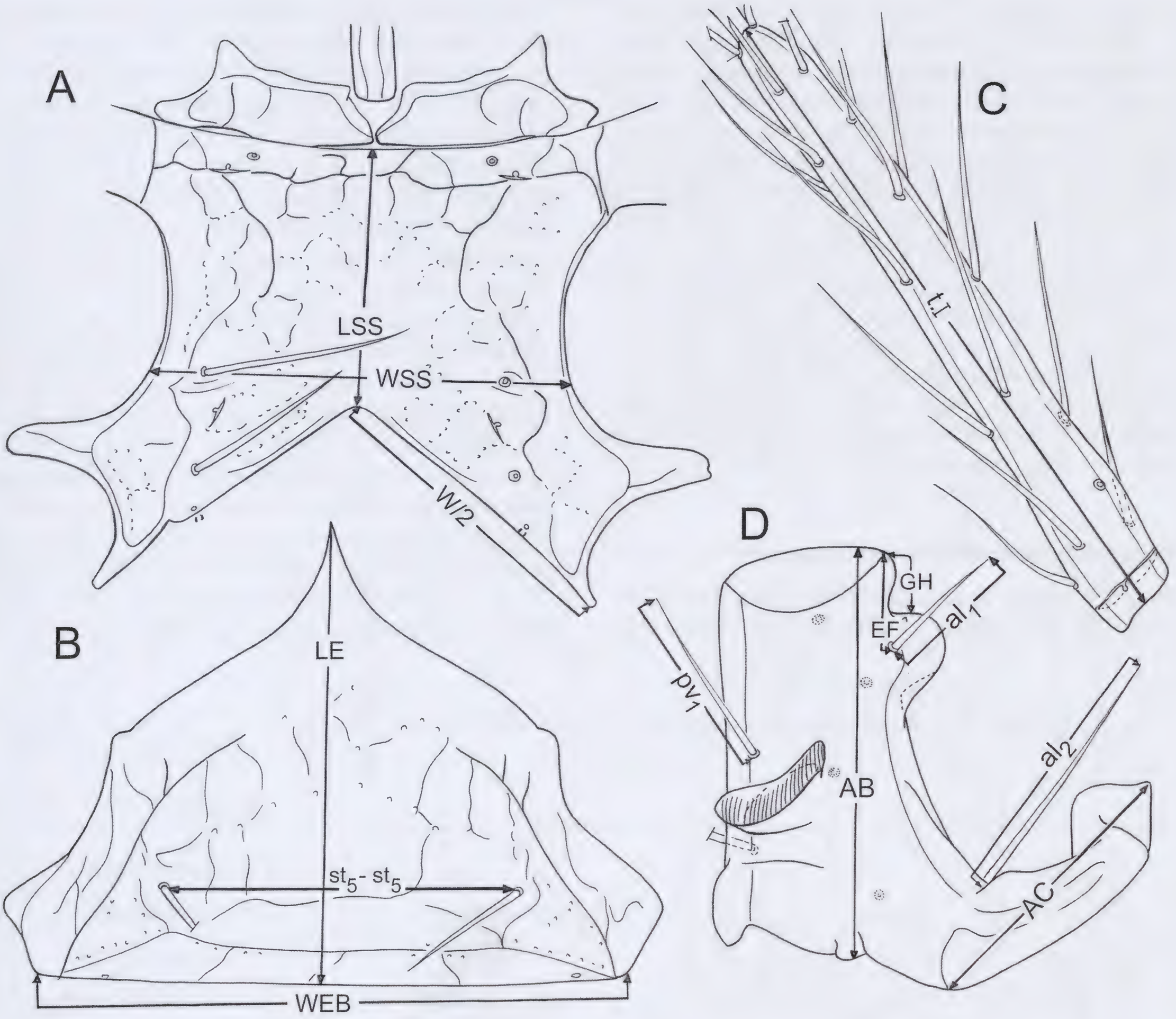

Fig. 1. *Pergamasus scorilai*; explanation of measurements taken from females (A-B) and males (C-D). (A) Sternal shield. (B) Epigynium. (C) Tarsus I. (D) Tibia II. For abbreviations see text and Table 1.

among each pair of populations using Welch's t-tests. For each sex we carried out a principal component analysis (PCA) as described before. This analysis allows representing the maximum of the multivariate variance in a reduced number of dimensions, each of them being a linear combination of the original variables (here: morphological measurements). The generalized squared Mahalanobis distance (D2) was calculated for all pairs of groups. This distance measures the separation of two groups in multidimensional space where all variables are scaled to have unit variance.

In an attempt to reduce the number of measurements necessary for species recognition, we implemented a variable selection process to retain only the most informative ones. To this end we compared the performance of different models (which included from one to all the morphological traits measured) using the Akaike information criterion (AIC). In particular, we used a backward selection approach, starting from a generalized linear model including all morphometric variables and removing one variable after the other until the model with the lowest AIC value possible was reached (Venables & Ripley, 2002). This stepwise procedure was carried out using the stepAIC function available in the MASS R package (Venables & Ripley, 2002).

RESULTS

Our analysis of all male morphometric characters for the 15 species in the *P. crassipes* species-group indicates that the morphometric characters traditionally used for species recognition does allow the separation of these taxa (Fig. 2). On the left side of the PCA, seven

species (*P. crassipes*, *P. dumitrescui* Juvara-Balş, 1970, *P. longicornis*, *P. palatortus* Athias-Henriot, 1967, *P. pinguicrus*, *P. buerebistai* and *P. similicornis* Athias-Henriot, 1967) exhibit relatively large AB, AC, t1, t4 and al2 measurements. Among the remaining species, three small-sized species (*P. caninatellus*, *P. laetus* Juvara-Balş, 1970 and *P. biharicus* Juvara-Balş, 1973) are isolated from others in the top-right corner of the PCA, while *P. truatellus* Athias-Henriot, 1967, in the bottom-right corner, is characterized by larger EF, GH, pv1 and al1 measurements. Finally, morphometric characters of *P. aequicornis* Athias-Henriot, 1967, *P. primorellus* Athias-Henriot, 1967, *P. decebali* and *P. scorilai* are quite similar (Fig. 2). However, these four species differ by morphological characteristics of tibia II and of the male chelicerae (Fig. 3A, F, L, M).

Morphological variability within species

Males: Variation is striking in the male tibia II of *P. decebali* and *P. scorilai*. A series of variants of the tibia II distal and proximal apophyses has been illustrated in *P. primorellus* (Athias-Henriot, 1967; fig. 250) and *P. longicornis* (Athias-Henriot, 1967; fig. 251). Juvara-Balş (1973, 1976) briefly described the variability of the proximal tibial apophysis in *P. scorilai*, *P. decebali*, *P. buerebistai* and *P. dumitrescui*.

In *P. scorilai* (n=91) the apex of the tibial apophysis, with a slightly invaginated spatula (n=15), is always more or less square. The form of the apical lobe is also subject to some variation: the upper edge is straight or weakly concave (n=19; Fig. 4A-B, I); the spatula possesses an acute external angle (n=31; Fig. 4C-D) or is trapezoidal with an elongated antiaxial edge (n=12; Fig. 4E-F); the antiaxial edge is considerably extended and the apex is rounded (n=11; Fig. 4G-H).

In *P. decebali* (n=31) the apex of the proximal apophysis, with a non-invaginated spatula, usually has the shape of a triangle that is more or less pointed (Fig. 3F), but in some specimens it is more trapezoidal (Juvara-Balş, 1973: fig. XI E'-E''). The diverse forms of species closely related to *P. scorilai* and *P. decebali* are illustrated in Fig. 3.

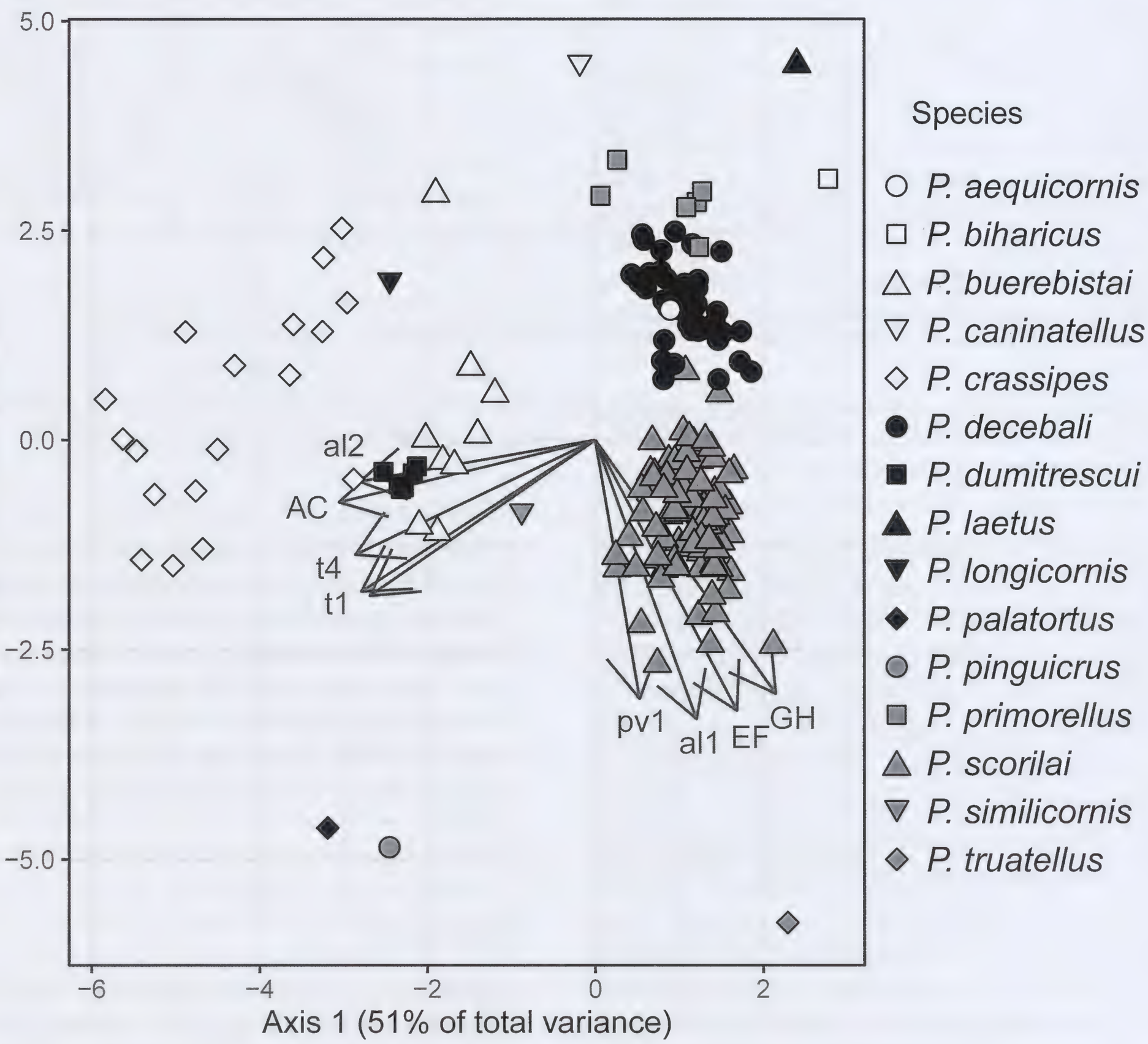

Fig. 2. Principal component analyses based on all morphometric characters of male individuals of the 15 species in the *Pergamasus crassipes* species-group. Individuals are represented by different symbols according to species.

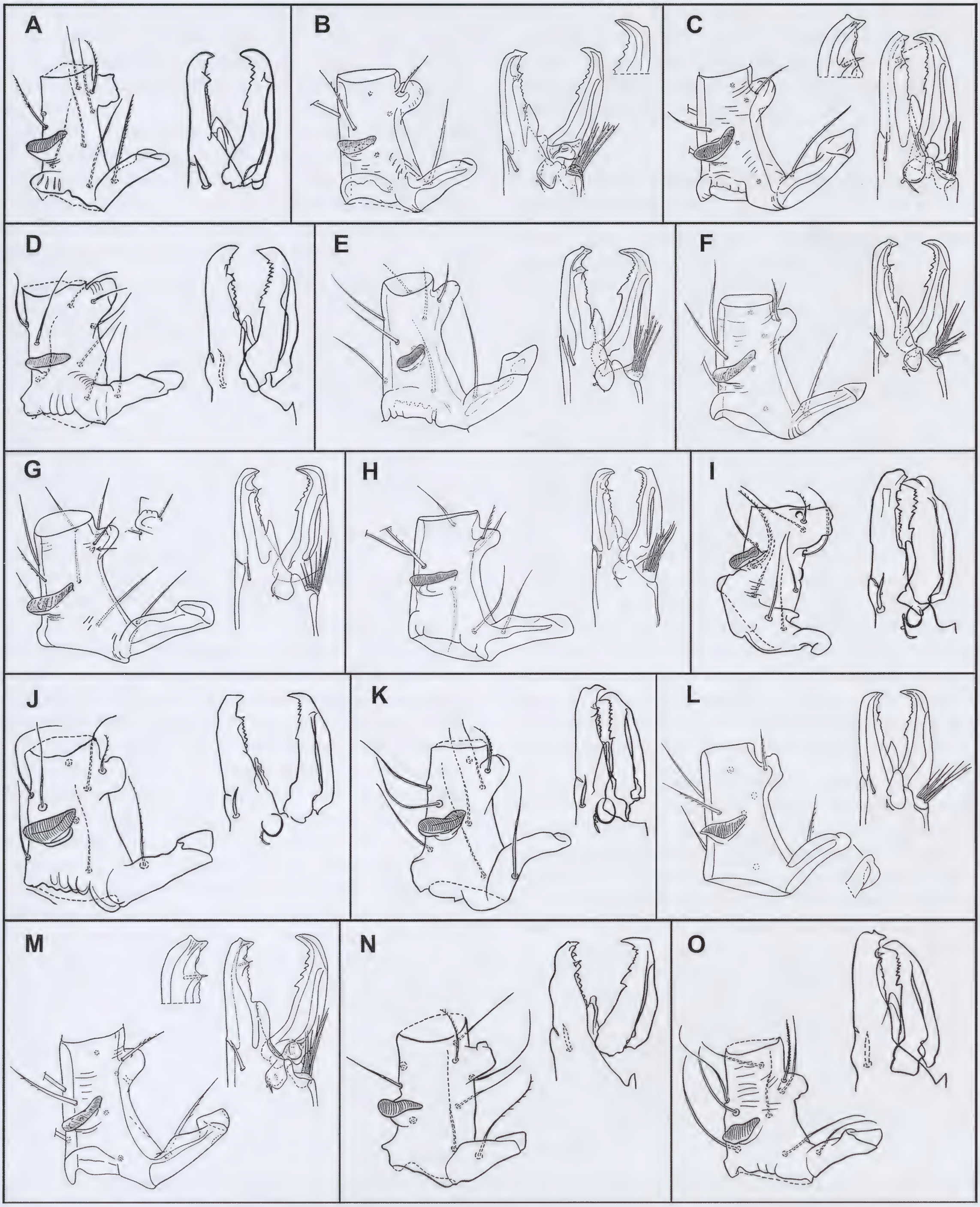

Fig. 3. Male tibia II (on the left) and male chelicerae (on the right) of *Pergamasus* spp. (A) *P. aequicornis*. (B) *P. biharicus*. (C) *P. buerebistai*. (D) *P. caninatellus*. (E) *P. crassipes*. (F) *P. decebali*. (G) *P. dumitrescui*. (H) *P. laetus*. (I) *P. longicornis*. (J) *P. pinguicrus*. (K) *P. palatortus*. (L) *P. primorellus*. (M) *P. scorilai*. (N) *P. similicornis*. (O) *P. truatellus*. Drawings in thick lines modified from Athias-Henriot, 1967 and drawings in thin lines from Juvara-Balş, 1970, 1973 or original.

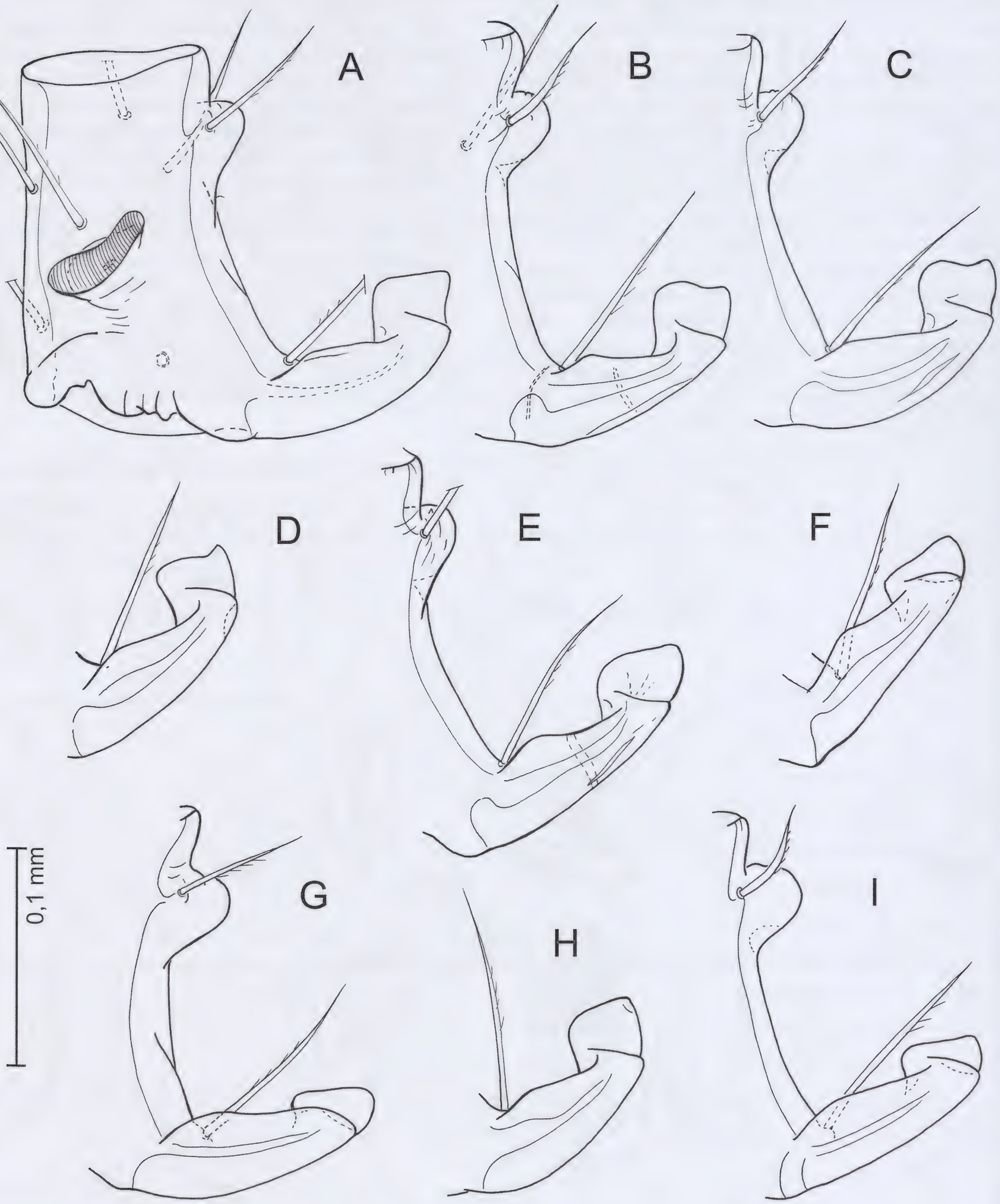

Fig. 4. Variations in the shape of the apex of the proximal apophysis of tibia II in males of *Pergamasus scorilai* from the type locality (Sucu Valley). (A) Tibia II. (B-I) The right side and apophysis of tibia II. Modified from Juvara-Balş, 1973.

In *P. buerebistai* the apical lobe is sub-quadrangular, with a pointed or mucronate apex (Fig. 3C), while in *P. dumitrescui* it is quadrangular (Fig. 3G), and in *P. biharicus* it constantly shows the shape of a club (Fig. 3B).

The form of the gnathotectum is equally variable in *P. scorilai*, *P. decebali* and *P. buerebistai*. In some individuals of these three species the five prongs are at the same level, while in other specimens the three middle prongs are more protruding than the lateral ones (Juvara-Balş, 1973: figs IV G-H, VIII B-C, XI B-C).

Females: An important character in the identification of females is the morphology of the endogynium. Variation can be observed in the size of the triangular process of the trabeculae, in the shape and size of the stipula, as well as in the number of denticles of the endogynial sack.

Variability in endogynial characteristics in *P. scorilai* is so pronounced that two morphotypes in the type series can be differentiated based on the following characteristics (Juvara-Balş, 1973: fig. VII):

- stipula with two branches, very large trabecular process, endogynial sack with denticles;
- stipula digitiform, only slightly enlarged trabeculae, endogynial sack devoid of denticles.

Among the 49 females of the type series, 23 have the stipula with two branches, 18 have a digitiform stipula and 8 have a stipula with intermediate forms. Intermediate forms are those with a stipula possessing less differentiated, smaller, or regressed branches. These forms are the extremes of a series of variants detected in many specimens from two large samples. In all studied populations of *P. scorilai* the form of the endogynium can significantly diverge from the typical morphology (Juvara-Balş, 1973: fig. VII A, F): on one hand by reduction of the two branches of the stipula to a digitiform one (Juvara-Balş, 1973: fig. VII D-F, I), and on the other by the triangular process of the trabeculae being reduced to form a simple edge paraxially (Juvara-Balş, 1973: fig. VII C, F). The latter polymorphism was observed at the individual level, with a specimen having one unarmed trabecula on one side and a triangular process on the other side (Juvara-Balş, 1973: fig. VII B).

Variation in the stipula is evident in *P. decebali* specimens collected in the western and southern Carpathians. Among the 31 specimens from the type-series, only four have an almost digitiform stipula with regressed branches, while 27, including the holotype, have a stipula with two short branches (Fig. 5E-G). The number of denticles of the endogynial sack is variable, and they may even lack in some specimens of *P. decebali* (Fig. 5G).

Pergamasus scorilai shows marked variation in the ornamentation of the sternal and epigynial shields. Some specimens have a marked reticulation and few dimples, whereas others have a strongly reduced reticulation with numerous dimples (Fig. 5C-D). Intermediate forms were found and all combinations of patterns are possible.

In *P. decebali* the reticulation of the sternal shield is accompanied by small dimples located below lyrifissure 2 and towards the lateral edges of this shield. The epigynial reticulation can be pronounced, but always is with dimples (Fig. 5A-B).

Morphometric variability across the three populations examined

Males: Some measurements differ between the two sampled populations of *P. scorilai* (Table 1 and Fig. 6). In particular, the length of tibia II (AB) is significantly greater in individuals from the Sucu Valley beech forest compared to those from Mt Mic spruce forest (Table 2). The length of the idiosoma, and distances EF and GH also differ significantly for both *P. scorilai* populations, but for these measurements the values were lower in individuals from Sucu Valley than in those from Mt Mic. The GH measurement of *P. scorilai* specimens from Sucu Valley have a smaller coefficient of variation (5.54%) than measurement of conspecific specimens from Mt Mic and specimens of *P. decebali* from the same biotope (spruce forest). The squared Mahalonobis distance (D2) calculated from eight characters leads to larger interspecific distances than intraspecific ones. Moreover, the distance between centroids of the type series of *P. decebali* and *P. scorilai* (D2 = 5.19), collected in different biotopes, is higher than the one measured between *P. decebali* and *P. scorilai* from the same biotope (D2 = 4.21). The distance between the two populations of *P. scorilai* is the smallest (D2 = 2.92).

Females: The morphological measurements of *P. scorilai* and *P. decebali* females show variation in several characters (Table 1 and Fig. 6). In particular, the length of idiosoma, epigynium and tarsi I and IV significantly differ between all populations (Table 2). *Pergamasus decebali* exhibits smaller values than *P. scorilai* for all these measurements. Within *P. scorilai*, the population from Sucu Valley beech forest has a smaller idiosoma and epigynium but larger tarsi than the population sampled in the Mt Mic spruce forest. The Mahalanobis distance is greatest (D2 = 4.87) for the type series of *P. decebali* and *P. scorilai* (Sucu Valley), intermediate (D2 = 4.50) for *P. decebali* and *P. scorilai* collected from the same biotope (at Mt Mic), and the lowest (D2 = 2.72) for the two populations of *P. scorilai*.

Morphometric discrimination of *P. scorilai* and *P. decebali*

Males: All morphological measurements, except the length of setae al2, significantly differ between males of *P. decebali* and *P. scorilai* (Table 2), the latter species being generally larger than the former (Table 1). However, there is no single morphological

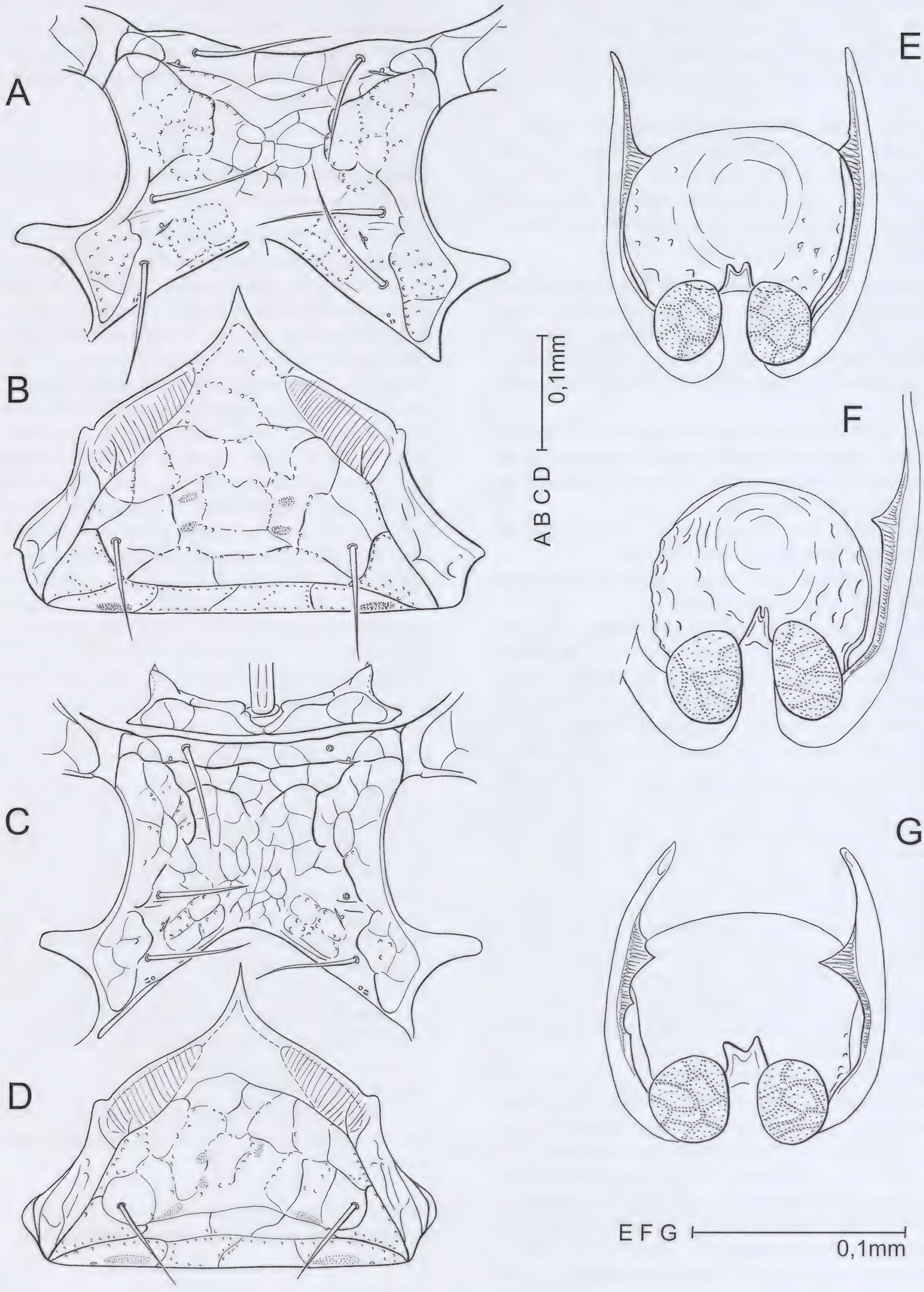

Fig. 5. Females of *Pergamasus decebali* (A-B, E-G) and of *P. scorilai* (C-D). (A, C) Sternal shield. (B, D) Epigynium. (E-G) Endogynium. Modified from Juvara-Balş, 1973.

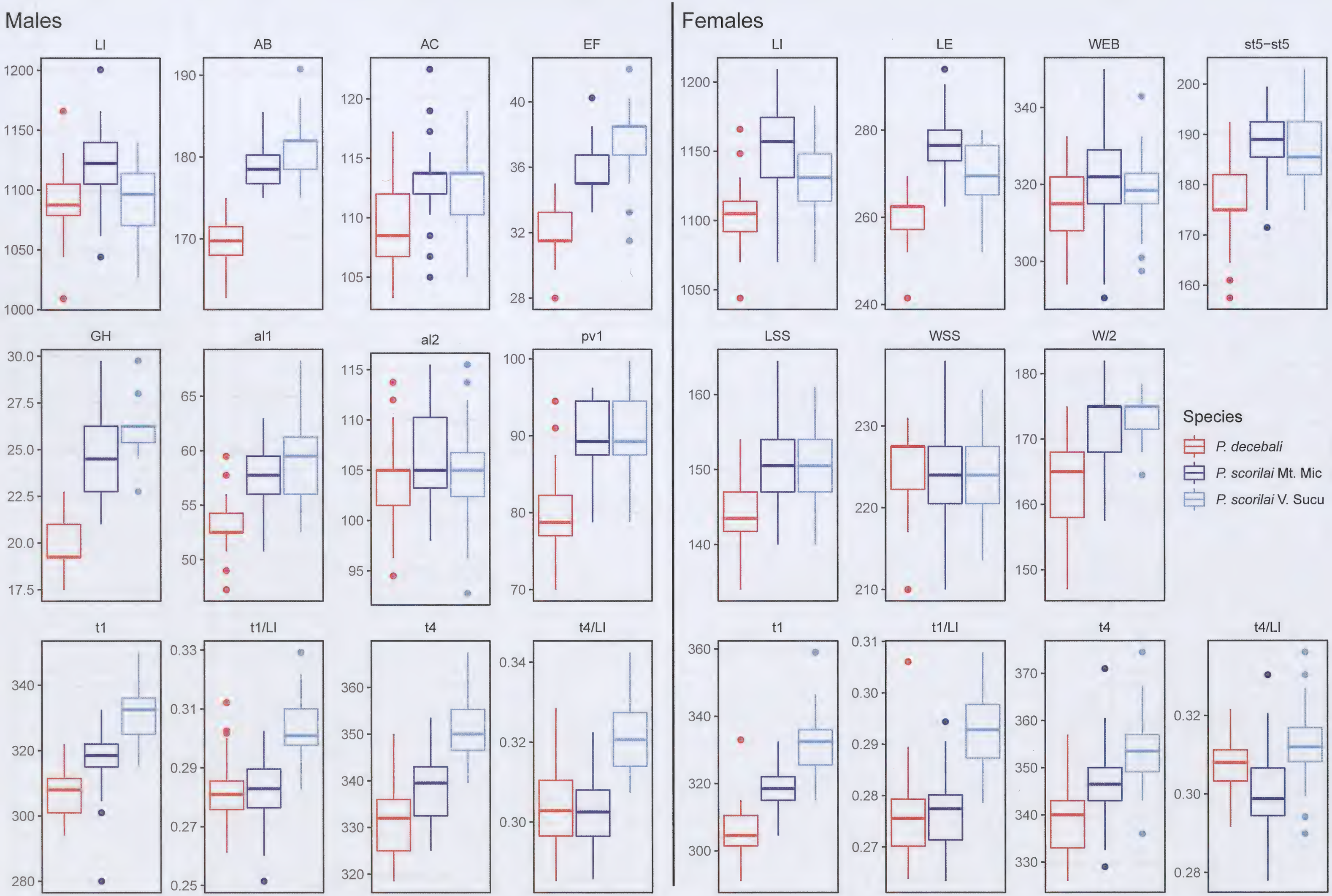

Fig. 6. Statistics of measurements taken from 133 males (left half) and 124 females (right half) of *Pergamasus decebali* (from one population) and *P. scorilai* (from two populations). Thick horizontal lines indicate the median, the boxes indicate the 25-75% range, the vertical lines indicate the 10-90% range; outliers are displayed as dots.

Table 1. Measurements (in µm) of *Pergamasus scorilai* and *P. decebali*. For each population and species the mean (M), standard deviation (SD), coefficient of variation (CV), minimum (min) and maximum (max) values are given.

FEMALES		*P. scorilai* from Sucu Valley (n=48)					*P. scorilai* from Mt Mic (n=45)					*P. scorilai* (n=93)					*P. decebali* (n=31)				
Measurement	Abbreviation	M	SD	CV	min	max	M	SD	CV	min	max	M	SD	CV	min	max	M	SD	CV	min	max
Length of idiosoma	LI	1132.07	24.54	2.17%	1070.00	1183.20	1152.99	28.12	2.44%	1070.00	1209.30	1142.19	28.22	2.47%	1070.00	1209.30	1103.90	23.52	2.13%	1044.00	1166.00
Length of epigynium	LE	269.28	7.59	2.82%	252.00	280.00	276.11	6.93	2.51%	262.50	294.00	272.59	8.01	2.94%	252.00	294.00	260.47	6.05	2.32%	241.50	269.50
Width of epigynium basis	WEB	318.79	8.78	2.75%	297.50	343.00	321.07	11.85	3.69%	290.50	350.00	319.89	10.39	3.25%	290.50	350.00	314.77	10.92	3.47%	294.00	332.50
Distance st5-st5	st5-st5	187.76	7.27	3.87%	175.00	203.00	189.16	7.00	3.70%	171.50	199.50	188.44	7.14	3.79%	171.50	203.00	176.24	7.37	4.18%	157.50	192.50
Length of sternal scutum	LSS	149.70	5.22	3.49%	140.00	161.00	150.97	5.15	3.41%	140.00	164.50	150.31	5.20	3.46%	140.00	164.50	144.44	4.25	2.94%	134.00	154.00
Width of sternal shield	WSS	224.15	5.05	2.25%	213.50	234.50	224.16	5.73	2.56%	210.00	238.00	224.15	5.36	2.39%	210.00	238.00	224.45	4.93	2.20%	210.00	231.00
Half width of posterior sternal scutum	W/2	173.03	3.38	1.95%	164.50	178.50	171.89	5.39	3.14%	157.50	182.00	172.48	4.48	2.60%	157.50	182.00	163.42	6.73	4.12%	147.00	175.00
Tarsus I	t1	331.23	8.39	2.53%	315.00	359.00	319.12	6.17	1.93%	304.50	332.50	325.37	9.55	2.93%	304.50	359.00	304.71	9.56	3.14%	291.00	333.00
Tarsus IV	t4	353.72	7.99	2.26%	336.00	374.50	346.19	8.20	2.37%	329.00	371.00	350.08	8.89	2.54%	329.00	374.50	339.23	7.47	2.20%	326.00	357.00

MALES		*P. scorilai* from Sucu Valley (n=47)					*P. scorilai* from Mt Mic (n=45)					*P. scorilai* (n=92)					*P. decebali* (n=41)				
Measurement	Abbreviation	M	SD	CV	min	max	M	SD	CV	min	max	M	SD	CV	min	max	M	SD	CV	min	max
Length of idiosoma	LI	1092.13	26.22	2.40%	1026.60	1139.70	1121.72	30.33	2.70%	1044.00	1200.60	1106.60	31.84	2.88%	1026.60	1200.60	1089.83	24.84	2.28%	1009.20	1165.80
Length of tibia II	AB	181.22	3.00	1.66%	175.00	190.75	178.58	2.77	1.55%	175.00	185.50	179.93	3.17	1.76%	175.00	190.75	169.96	2.60	1.53%	162.75	175.00
Length of proximal apophysis	AC	112.56	3.54	3.14%	105.00	119.00	113.52	3.59	3.16%	105.00	122.50	113.03	3.58	3.17%	105.00	122.50	109.23	3.27	3.00%	103.25	117.25
Distance between seta al1 insertion and tibial margin	EF	37.83	1.98	5.24%	31.50	42.00	36.13	1.63	4.52%	33.25	40.25	37.00	2.00	5.41%	31.50	42.00	32.05	1.85	5.78%	28.00	35.00
Distance between distal apophysis and tibial margin	GH	26.03	1.44	5.54%	22.75	29.75	24.85	1.92	7.74%	21.00	29.75	25.45	1.79	7.02%	21.00	29.75	19.72	1.52	7.69%	17.50	22.75
Length of seta al1	al1	58.72	3.30	5.62%	52.50	68.25	57.79	2.75	4.77%	50.75	63.00	58.26	3.06	5.26%	50.75	68.25	53.18	2.68	5.04%	47.25	59.50
Length of seta al2	al2	104.85	4.66	4.44%	92.75	115.50	106.17	4.57	4.30%	98.00	115.50	105.49	4.64	4.39%	92.75	115.50	104.27	3.95	3.79%	94.50	113.75
Length of seta pv1	pv1	90.03	4.97	5.52%	78.75	99.75	89.72	4.71	5.25%	78.75	96.25	89.88	4.82	5.37%	78.75	99.75	79.43	4.68	5.89%	70.00	94.50
Tarsus I	t1	330.87	8.55	2.58%	315.00	350.00	317.09	8.41	2.65%	280.00	332.50	324.13	10.92	3.37%	280.00	350.00	306.98	6.97	2.27%	294.00	322.00
Tarsus IV	t4	351.49	6.48	1.84%	339.50	367.50	339.41	6.42	1.89%	325.00	353.50	345.58	8.83	2.56%	325.00	367.50	331.10	7.56	2.28%	318.50	350.00

Table 2. Welch's *t*-tests for equality of means. Statistical tests were performed for all pairs of species and populations.

FEMALES		*P. scorilai* from Sucu Valley vs. *P. scorilai* from Mt Mic	*P. scorilai* from Sucu Valley vs. *P. decebali*	*P. scorilai* from Mt Mic vs. *P. decebali*	*P. scorilai* vs. *P. decebali*
Measurement	Abbreviation				
Length of idiosoma	LI	<0.001	<0.001	<0.001	<0.001
Length of epigynium	LE	<0.001	<0.001	<0.001	<0.001
Width of epigynium basis	WEB	0.29	0.08	<0.05	<0.05
Distance *st5-st5*	st5-st5	0.35	<0.001	<0.001	<0.001
Length of sternal scutum	LSS	0.24	<0.001	<0.001	<0.001
Width of sternal shield	WSS	0.99	0.79	0.82	0.77
Half width of posterior sternal scutum	W/2	0.22	<0.001	<0.001	<0.001
Tarsus I	t1	<0.001	<0.001	<0.001	<0.001
Tarsus IV	t4	<0.001	<0.001	<0.001	<0.001
Tarsus I/length of idiosoma	t1/LI	<0.001	<0.001	0.67	<0.001
Tarsus IV/length of idiosoma	t4/LI	<0.001	<0.01	<0.001	0.68
MALES		*P. scorilai* from Sucu Valley vs. *P. scorilai* from Mt Mic	*P. scorilai* from Sucu Valley vs. *P. decebali*	*P. scorilai* from Mt Mic vs. *P. decebali*	*P. scorilai* vs. *P. decebali*
Measurement	Abbreviation				
Length of idiosoma	LI	<0.001	0.67	<0.001	<0.01
Length of tibia II	AB	<0.001	<0.001	<0.001	<0.001
Length of proximal apophysis	AC	0.20	<0.001	<0.001	<0.001
Distance between seta al1 insertion and tibial margin	EF	<0.001	<0.001	<0.001	<0.001
Distance between distal apophysis and tibial margin	GH	<0.01	<0.001	<0.001	<0.001
Length of seta al1	al1	0.15	<0.001	<0.001	<0.001
Length of seta al2	al2	0.17	0.53	<0.05	0.12
Length of seta pv1	pv1	0.76	<0.001	<0.001	<0.001
Tarsus I	t1	<0.001	<0.001	<0.001	<0.001
Tarsus IV	t4	<0.001	<0.001	<0.001	<0.001
Tarsus I/length of idiosoma	t1/LI	<0.001	<0.001	0.63	<0.001
Tarsus IV/length of idiosoma	t4/LI	<0.001	<0.001	0.54	<0.001

measurement allowing the distinction of these two species because all overlapped to different extents (Fig. 6). Remarkably, the length of tibia II (AB) barely overlaps between the two species, and only so for the marginal value of 175.0 µm. The length of the proximal apophysis AC also has relatively low coefficients of variability within *P. scorilai* (3.14-3.16%) and *P. decebali* (3.00%), but important overlaps in values exist between both species. The distance GH has the largest coefficients of variation, especially for *P. decebali* and the *P. scorilai* population from Mt Mic (7.74% and 7.69%, respectively). However, this character seems interesting for species recognition as values only marginally overlap. The two ratios (t1/LI and t4/LI) also significantly differ between species, although this difference disappears when restricting the comparison of *P. decebali* with *P. scorilai* from Mt Mic only (Table 2).

The PCA analysis resulted in a perfect segregation of *P. decebali* from *P. scorilai* along the first multivariate axis, which expresses about half of the total variance (Fig. 7). *Pergamasus scorilai* individuals exhibit larger values for many tibial measurements (AB, GH, EF, pv1 and al1). The length of the idiosoma, although statistically significantly different between the two species, was mostly contributing to the second axis and thus is not very useful for species recognition. The length of seta al2 is also contributing to the second axis, but it mostly represents intraspecific variation as it does not differ between both species.

The best model identified by the algorithm using the AIC measure contains only two measurements: the length of tibia II (AB) and the length of setae al1 (al1). The intercept and coefficient of the selected linear model provided the following discriminant function: 15476.0 - 80.04 × AB - 26.68 × al1. The discriminant score calculated using this function was negative when applied to measurements of male *P. scorilai* specimens, and positive for *P. decebali* males. We propose a simplified, yet effective function inspired from the previous for species discrimination based on male specimens: 155 - 0.8 × AB - 0.3 × al1.

Females: As in males, all morphological measurements but one (the width of the sternal shield) significantly differ between females of the larger *P. scorilai* and those of the smaller species *P. decebali* (Tables 1-2). For the eight measured characters the coefficient of variability ranges from 1.93% to 4.18% and is in general smaller than the values observed in males (1.53%-7.74%). However, all morphological characters overlap considerably between both species, so that no single character or combination of two characters can be used for species recognition. As in males, the ratio between the tarsus I and the idiosomal length (t1/LI) significantly differs between species, but not when only considering *P. scorilai* from Mt Mic (Table 2). The ratio between the tarsus IV and the idiosomal length (t1V/LI) does not significantly differ between species, but significant differences were recovered when considering populations, because *P. scorilai* from Mt Mic and from Sucu Valley have lower and greater values, respectively, than *P. decebali* (Fig. 6).

In females species discrimination was not completely achieved in the bidimensional space maximising the total variance (Fig. 7). Similar to the PCA conducted on males, the first axis carries over 40% of the total variance, with *P. scorilai* individuals having lower values along this axis than those of *P. decebali*. This position on the first axis correlates with higher values of many morphological measurements, including lengths of idiosoma, epigynium, tarsi and sternal scutum (Fig. 7).

The best model identified by the algorithm using the AIC measure contains no less than six measurements. The intercept and coefficient of the selected model provides the following discriminant function: 37020.41735 - 25.30969 × LI - 113.96783 × LSS + 143.80938 × WSS - 73.66982 × W/2 - 89.42145 × t1 + 46.84512 × t4. The discriminant score calculated using this function is negative when applied to measurements of female *P. scorilai* specimens, and positive for *P. decebali* females. We propose an even more simplified, yet efficient function inspired from the previous one: 370.204 - 0.253 × LI - 1.14 × LSS + 1.438 × WSS - 0.737 × W/2 - 0.894 × t1 + 0.468 × t4.

DISCUSSION

Overview of the *Pergamasus crassipes* species-group

Based on male characteristics, Athias-Henriot (1967) and Juvara-Balş (1970, 1973) listed as many as 15 described species in the *Pergamasus crassipes* species-group: *aequicornis*, *biharicus*, *buerebistai*, *caninatellus*, *crassipes*, *decebali*, *dumitrescui*, *laetus*, *longicornis*, *pinguicrus*, *palatortus*, *primorellus*, *scorilai*, *similicornis*, and *truatellus*. Males of most species can be easily separated using the nine measurements retained in our analyses (Fig. 2). The measurements of *P. aequicornis* from Connecticut, USA are similar to those of *P. decebali* from Romania (Fig. 2). However, *P. aequicornis* is very different from *P. decebali* by the

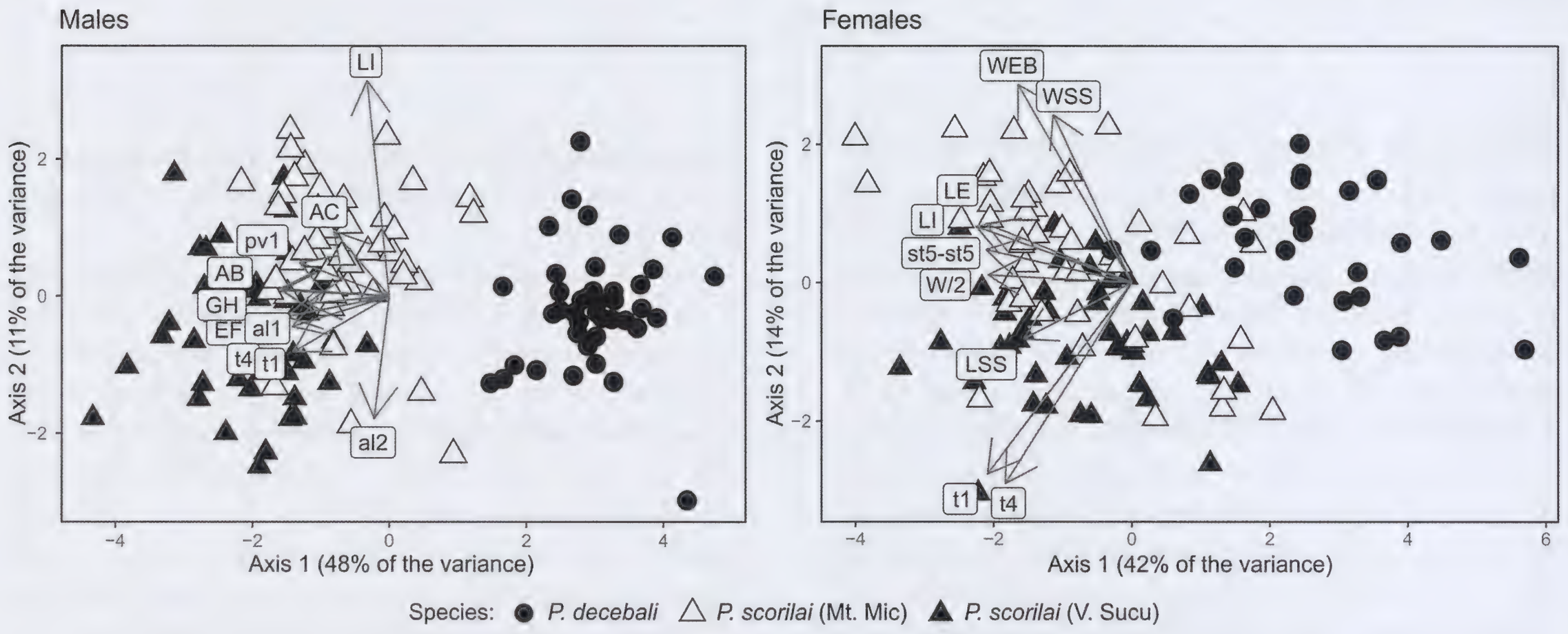

Fig. 7. Principal component analyses based on all morphometric characters of male and female *Pergamasus decebali* and *P. scorilai* individuals examined. Individuals are represented by different symbols according to species and geographical origin.

morphology of the chelicera and of the apophysis of tibial II (Fig. 3A cf. Fig. 3F). *Pergamasus primorellus* also lies close to small *P. decebali* specimens in the ACP representation. Males of the two species differ by the shape of the apophyses of tibia II (Fig. 3L cf. Fig. 3F), as well by the shape of the endogynium in females.

Finally, the case of *P. instipatus*, a species described from a single female, deserves special attention. Athias-Henriot (1967) considered the corresponding male to be unknown and thus the species was not assigned to any of the species-groups based on male characteristics. In the collection of Athias-Henriot held in the Natural History Museum of Geneva three presumably conspecific specimens from the same locality (Seppenbauer, northwestern Carinthia, Austria) were found. One female and one male (AN260 and AN261, respectively) identified as *P. caninatellus* were collected in the same sample under composite flowers, while the third specimen was a female (AK766) collected under *Trifolium* and *Plantago* at the same locality. The latter individual was tentatively identified as "cf. *instipatus*" in Athias-Henriot's field notebook, which was then corrected as "*caninatellus*". The comparison of these two *P. caninatellus* female specimens collected at Seppenbauer together with the holotype of *P. instipatus* shows that both nominal species are indistinguishable. Therefore we here place *P. instipatus* Athias-Henriot, 1967 in the synonymy of *P. caninatellus*, a conclusion that Athias-Henriot seemingly reached herself as indicated in her field notebook.

Variability and recognition of *Pergamasus scorilai* and *P. decebali*

Taxa are named and given representative type specimens, but they are also populations and aggregates of populations (Mayr, 1969). Therefore, assessment of the morphological variability and statistical analysis of the morphometric characteristics should be mandatory for taxonomic work. In particular, it is necessary to specify the limits of variability of qualitative and quantitative characters, especially in species with a similar morphology.

The morphological and morphometric analysis of over 250 specimens from Romania revealed that a fair amount of intraspecific morphological variability occurs in two similar species, *P. scorilai* and *P. decebali*. The morphological study of an extensive material allowed us to describe distinctive morphological characters, either found on tibia II or in the endogynium of males and females, respectively. Morphometric values overlap between both species for most of the other morphological measurements, complicating species recognition and giving some credit to previously expressed opinions which considered the two species as conspecific (Karg, 1993). However, multivariate analyses clearly discriminate two morphometric groups, independent of the biotope they were collected in (Fig. 7) and are consistent with the morphology-based concepts of the two nominal species. Accordingly, the morphometric variation remains smaller at the intraspecific level than between the two species. Based on a combination of a few morphometric characters (two in males, six in females), we demonstrate that the species *P. decebali* and *P. scorilai* can be unambiguously separated. These results show the value of the characters that were established by Athias-Henriot (1967) for the diagnosis of the taxa included in the *Pergamasus crassipes* species-group.

Analysis of the variables showed that most of the retained male characteristics can be used for species distinction, especially the length of tibia II and the length of setae al1. The size of setae al2 does not significantly differ between the two species, and the length of the idiosoma overlaps greatly although the individual means are significantly different. The morphological analysis revealed other essential characters for the identification of males, which could not be included in our morphometric analyses: (i) the shape of the apex of the movable or fixed chelicera digit; (ii) the shape of the proximal tibial apophysis of leg II (AC) and especially its apical lobe, which although variable is showing patterns specific to each species; (iii) trochanter IV protrusions on the dorsal and ventral sides. In females the variable selection approach consistently requires as many as six measurements that allow species differentiation, with a weaker segregation of individuals in the multivariate analysis than observed in males. Interestingly, the width of the sternal scutum was retained in the discriminant function, although it was the only character which did not statistically differ between both species. Hence it appears that many additional morphological measurements should always be accounted for when diagnosing or describing females. Diagnoses of females of *P. scorilai* and *P. decebali* must be emended mainly by accounting for details of the endogynium, the shape of the protrusions of trochanter IV, and to a lesser extent the sterno-genital cuticle ornamentation. In females the phenotypes of the same species are so different that if one choses a holotype without examining the variation of the endogynium, one would be convinced that other conspecific females belong to different species (Juvara-Balş, 1973: fig. VII A, F). Another feature that characterizes *P. decebali* females from the southern Carpathians lie in the reduced size of the protuberance on trochanter IV. Unfortunately, this character cannot be used in geographical regions where *P. decebali* coexist with *P. scorilai* (e.g., the western Carpathians - Mt Apuseni) since both species have a similar marked protuberance on trochanter IV in these areas (Juvara-Balş, 1973; fig. IV. I and fig. XI. I). The morphometric characters most useful for the identification of females of these two species are the half-length of the posterior sternal margin, and the lengths of sternal scutum, epigynium, tarsus I and tarsus IV.

In males and females *P. decebali* turned out to be more similar to *P. scorilai* from Mt Mic than to *P. scorilai* from Sucu Valley. We assume that this is due to some form of ecological convergence, as the two first mentioned populations were sampled in spruce forests situated above 1000 m a.s.l., while the Sucu Valley population occurs in a lowland beech forest. In particular, relative leg measurements of females (t1/LI and t4/LI) were lower in individuals sampled at higher elevations and higher in the population from lowlands. Although based on two sampling sites, these observations are congruent with the Allen's rule which postulates that "protruding body parts […] are relatively shorter in cooler parts of the range of a species than in warmer parts" (Ray, 1960). Although originally formulated for thermoregulating animals, this rule was also found to apply to various arthropod groups (Ray, 1960; Bidau & Martí, 2008).

Pending questions regarding other species

Even partial knowledge of variability raises new problems concerning other species. One case involves *P. crassipes* and *P. primorellus*, which are similar and difficult to separate without taking into account the variability of the endogynium of females and that of the proximal apophysis of tibia II as well as other morphometric characters in males. Another case concerns the great resemblance between *P. dumitrescui* and *P. pinguicrus* which casts doubts on the species status of corresponding populations found in Romania. *Pergamasus dumitrescui* specimens from the southern Carpathian (Bucegi Massif; Mount Baiului) are morphologically similar to *P. pinguicrus* specimens described from Austria (Niedere Tauern, Admont).

The corresponding type series justified the description of these two nominal species at the time. In the description of *P. dumitrescui*, Juvara-Balş (1970) specified that this species differs from *P. pinguicrus* "by its smaller dimensions, the number of hypostomial ridges, and the lack of accessory denticles between the prongs of the gnathotectum". Studying other specimens from Austria (in the collection of Athias-Henriot) and Romania (eastern and southern Carpathian; Moldavian Hills) we observed that the variation of the endogynium (size of the stipula, denticles of the endogynial sack) and the degree of ornamentation of the sclerocuticle were similar in these two species. The male characteristics are fairly constant. The differences in males are expressed only in the distal apophysis of the tibia II which have a denticle at the base of setae al1 in *P. dumitrescui* but lack this denticle in *P. pinguicrus*.

The presented data lead us to consider these two nominal taxa as true species, but the variation of each is primarily statistical, with the studied specimens from populations in Romania being much smaller than those from populations in Austria. The upper limits of values of many characters does not overlap with the lower limits of *P. pinguicrus* characters (Juvara-Balş, pers. obs.). However, the status of these species or subspecies is unclear until two points are clarified. First, there is a need to establish the variability of *P. pinguicrus* from the type locality in Austria (Leichenberg bei Admont). Second, the geographical ranges of the two taxa still need to be delimitated. The Slovenian Alps, the Dinaric Range and the Balkan Peninsula are still "terra incognita" with respect to these taxa. Intergradation zones could exist, and a clinal variation cannot be excluded.

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REFERENCES

Athias-Henriot C. 1967. Observations sur les *Pergamasus* II: sous-genre *Pergamasus* Berl., 1904 (Acariens Anactinotriches: Parasitidae). *Acarologia* 9: 669-761.

Athias-Henriot C. 1968. Observations sur les *Pergamasus* IV. Un essai de coordination de la taxonomie et de la chorologie du sous-genre *Pergamasus* s. s. (Acariens Anactinotriches: Parasitidae). *Acarologia* 10: 181-190.

Athias-Henriot C. 1971. *Paragamasus* (*Tanygamasus*) *probsti* (Oudemans) (systématique, géographie) avec quelques mises au point synonymiques (Arachnides, Gamasides tocospermiques, Parasitidae). *Zoologische Mededelingen* 45(16): 167-179.

Berlese A. 1903. Acari nuovi. Manipulus Ius. *Redia* 1: 235-252.

Berlese A. 1906. Monografia del genere *Gamasus* Latr. *Redia* 3: 65-304.

Bhattacharyya S.K. 1963. A revision of the British mites of the genus *Pergamasus* Berlese s. lat. (Acari: Mesostigmata). *Bulletin of the British Museum (Natural History)* 11: 131-242.

Bidau C.J., Martí D.A. 2008. A test of Allen's rule in ectotherms: the case of two South American melanopline grasshoppers (Orthoptera: Acrididae) with partially overlapping geographic ranges. *Neotropical Entomology* 37: 370-380. DOI: 10.1590/S1519-566X2008000400004

Dielmann M. 1991. Computer in acarine taxonomy: a method for systematical analysis of the genus *Pergamasus* (Acarina: Mesostigmata) (pp. 239-248). *In:* Dusbabek F., Bukva V. (eds), Modern Acarology, 2. *Academia Prague and SPB Academic Publishing*, *The Hague*, 1504 pp.

Dray S., Dufour A. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22: 1-20. DOI: 10.18637/jss.v022.i04

Hrúzová K., Fend'a P. 2018. The family Parasitidae (Acari: Mesostigmata) - history, current problems and challenges. *Acarologia* 58: 25-42. DOI: 10.24349/acarologia/20184280

Hull J.E. 1918. Terrestrial Acari of the Tyne Province. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne* 5(1): 13-88.

Juvara-Balş I. 1970. Trois nouvelles espèces de *Pergamasus* Berlese s. str. de Roumanie (Acariens Anactinotriches-Parasitidae). *Acarologia* 12(2): 221-233.

Juvara-Balş I. 1973. Quatre nouvelles espèces de *Pergamasus* Berlese de Roumanie (Acarina Anactinotrichida-Parasitidae). *Travaux de l'Institut de Spéologie Emile Racovitza* 12: 139-165.

Juvara-Balş I. 1976. Contribution à la connaissance des genres *Pergamasus* Berlese et *Amblygamasus* Berlese de Roumanie. *Travaux de l'Institut de Spéologie Émile Racovitza* 15: 17-52.

Karg W. 1993. Acari (Acarina), Milben Parasitiformes (Anactinochaeta), Cohors Gamasina Leach. Raubmilben. *Die Tierwelt Deutschlands* 59: 1-475.

Latreille P.A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Tome premier. *F. Dufart, Paris*, 394 pp.

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio Decima, Reformata. Tomus I. *Laurentii Salvii, Holmiae*, ii + 824 pp.

Mayr E. 1969. Principles of systematic zoology. *McGraw-Hill Book Co., New York*, 428 pp.

Micherdzinski W. 1969. Die Familie Parasitidae Oudemans 1901 (Acarina, Mesostigmata). *Panstwowe Wydawnictwo Naukowe, Krakow*, 690 pp.

R Core Team 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at https://www.R-project.org/

Ray C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology* 106: 85-108. DOI: 10.1002/jmor.1051060104

Schweizer M. 1961. Die Landmilben der Schweiz (Mittelland, Jura und Alpen). Parasitiformes Reuter. *Denkschriften der Schweizerischen Naturforschenden Gesellschaft* 84: 1-207.

Venables W.N., Ripley B.D. 2002. Modern applied statistics with S-PLUS. 4th edition. *Springer Science & Business Media, New York*, xi + 501 pp.

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Notes on the genus *Ctenoneura* Hanitsch, 1925 with description of six new species (Dictyoptera: Corydiidae)

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Abstract: Six new species of the genus *Ctenoneura* are presented: *C. complicata* sp. nov., *C. virgata* sp. nov., *C. asymmetrica* sp. nov., *C. emarginata* sp. nov., *C. orlovi* sp. nov. and *C. gorochovi* sp. nov. Morphology-based descriptions of the new species are given. Some questions concerning morphology and the taxonomic position of the genus *Ctenoneura* are briefly discussed. Changes in the method of working with small and weakly sclerotized cockroaches are proposed.

Keywords: Cockroaches - morphology - taxonomy.

INTRODUCTION

The genus *Ctenoneura* Hanitsch, 1925 includes small and morphologically very specialized cockroaches (Hanitsch, 1929, 1932; Princis, 1954, 1967; Bey-Bienko, 1957, 1969; Roth, 1993, 1995; Qiu *et al.*, 2017). At first glance, representatives of the genus are more similar to small ectobiids than to other members of the family Corydiidae. The genus is taxonomically very isolated, so at present it is impossible to identify the taxon which is closest to it. Molecular data may shed some light on the systematic position of the genus in the future.
The publications of Roth (1993) and Qiu *et al.* (2017) are especially valuable for the study of *Ctenoneura*. These cockroaches are rare in scientific collections, although they appear to be widespread in South-East Asia. Representatives of the genus are distributed from Burma and southern China via the Malay Peninsula, Sumatra and Java to Borneo (Beccaloni, 2014).

MATERIAL AND METHODS

In my opinion, the method of working with small and weakly sclerotized cockroaches should differ from the one currently in use. Such cockroaches should not be pinned and dried. Pinned and dried specimens are usually deformed and very difficult to study. I prefer to collect, study and keep such specimens and its body parts in alcohol or other kinds of fixing liquid. This applies to all small and delicate cockroaches, and even more so to very fragile representatives of the genus *Ctenoneura*. Also, I do not recommend mounting the structures of the genital complex (i.e. male genitalia, anal plate, hypandrium and other adjacent structures) on microscope slides because it makes them very difficult to study. First, because the structures of the genital complex are very often deformed on microscope slides. Second, because the slide-mounted genital structures are fixed and immovable, and therefore impossible to examine from all angles. All this makes it extremely difficult or impossible to reconstruct complex three-dimensional structures often formed by the sclerites of the genitalia of cockroaches.
The availability of only unique specimens limited my ability to dissect and study such complex structures, like the right phallomere of the male genitalia, in detail. Therefore I had to limit myself to simplified drawings only.
The material studied (specimens and dissected body parts) is kept in 70% ethanol. The morphological structures were dissected and examined in Petri dishes under alcohol. The structures of the male genitalia were treated with alkali using the standard technique for removing soft tissues (Anisyutkin *et al.*, 2013).
The drawings were made by means of a drawing tube on a Leica MZ 16 binocular microscope and with an MBS-10 binocular microscope.
Rehn's (1951) terminology of tegmina and wing venation is used. The description of anterior margin of fore femur armament follows Bey-Bienko (1950) and Roth (2003). The terminology of male genital sclerites follows Klass (1997), with some modifications according to Qiu *et al.* (2017) and my previous papers. Terms introduced by the author are given in quotation marks.
The material studied is deposited in the Muséum

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d'histoire naturelle, Geneva, Switzerland (MHNG) and in the Zoological Institute of the Russian Academy of Sciences in Saint-Petersburg, Russia (ZIN).

Abbreviation used in the figures (see text for further explanations):

1pl. - 1st plical vein of hind wing (terminology after Rehn, 1951);
2pl. - 2nd plical vein of hind wing (terminology after Rehn, 1951);
3pl. - 3rd plical vein of hind wing (terminology after Rehn, 1951);
1scl. - additional sclerite of male genitalia;
1st.pr., 2nd.pr., 3rd.pr., 4.pr., 5.pr., 6.pr. - outgrowths of posterior margin of hypandrium;
Ant.R.rami - area of anterior branches of radius vein of hind wing (terminology after Rehn, 1951);
CuA - area of cubitus anterior vein branches (terminology after Rehn, 1951);
CuP - cubitus posterior vein (= plical furrow *sensu* Rehn, 1951);
eds. - extending structure of subgenital sclerite of male genitalia (terminology after Qiu *et al.*, 2017);
f.scl. - "folded sclerite" (*ldp+lvp sensu* Qiu *et al.*, 2017) of male genitalia;
i.v. - intercalary vein of tegmen (terminology after Roth, 1993);
l.p.a. - left posterolateral corner of hypandrium;
l.sty. - left stylus;
L3 - sclerite of male genitalia;
M - area of media vein branches;
par. - paraproct;
pv. - pv-sclerite;
R - area of radius vein branches;
r.p.a. - right posterolateral corner of hypandrium;
r.sty. - right stylus;
R3 - sclerite of male genitalia;
Sc - area of subcosta vein branches;
scl. - additional sclerite of male genitalia;
sgs. - subgenital sclerite (terminology after Qiu *et al.*, 2017) of male genitalia;
t.o. - triangular outgrowth of hypandrium;
tvs. - transverse sclerite of male genitalia (terminology after Qiu *et al.*, 2017).

TAXONOMIC PART

Genus *Ctenoneura* Hanitsch, 1925

Type species: *Ctenoneura major* Hanitsch, 1925, by subsequent designation (Princis, 1950).

Remarks: The genus *Ctenoneura* was described by Hanitsch (1925) and revised by Roth (1993) and Qiu *et al.* (2017). It includes small cockroaches of untypical appearance for the family Corydiidae (Figs 1-12). These cockroaches are similar to small representatives of the family Ectobiidae. In fact, the placement in Corydiidae is supported by the presence of a folded anal area of the hind wing (Fig. 21). However, this character also occurs independently, as shown for the blaberid genus *Miroblatta* Shelford, 1906 (Grandcolas, 1993a). The male genitalia of *Ctenoneura* are so strongly reduced and modified (Figs 27, 34, 40, 47, 55, 63) that it is difficult to homologize its structures.

In this paper I principally follow Qiu *et al.* (2017), who first described the male genitalia of *Ctenoneura*, in naming the male genital sclerites. Nevertheless, in my opinion only the homology of the R3 sclerite is undisputed. The plate-like and curved sclerite R3 is common not only in species of the Corydiidae, for instance representatives of the genera *Polyphaga* Brullé, 1835, *Therea* Billberg, 1820 and *Tivia* Walker, 1869 (see Klass, 1997; Qiu *et al.*, 2019), but also in species of the Cryptocercidae (see Klass, 1997), of Blattidae, for instance representatives of the genera *Periplaneta* Burmeister, 1838, *Macrostylopyga* Anisyutkin, Anichkin & Nguyen, 2013 and *Duchailluia* Rehn, 1933 (see Klass, 1997; Anisyutkin *et al.*, 2013; Anisyutkin, 2014; Anisyutkin & Telnov, 2018), of Tryonicidae (see Klass, 1997), of Lamproblattidae (see Klass, 1997), of Anaplectidae (see Klass, 1997) and of Nocticolidae, for instance representatives of the genus *Nocticola* Bolivar, 1892 (see Andersen & Kjaerandsen, 1995). The homologization of the other structures of the male genitalia needs confirmation. To resolve the problem of homologization of male genitalia structures, intermediate forms between *Ctenoneura* and coridiids with more typical genitalia are required, if such taxa exist. It may also be possible to extract data from the ontogenetic development of these cockroaches.

In my opinion, the subgenital sclerite (Figs 27, 31, 40, 47, 49, 53, *sgs.*) is a structure of the male genitalia, not part of the hypandrium (subgenital plate after Qiu *et al.*, 2017). In the specimens I studied and in the drawings of Qiu *et al.* (2017) there is no evidence for an attachment of this structure to the hypandrium; only the distal part of the subgenital sclerite (*eds.* - extending structure after Qiu *et al.*, 2017) can be overlapped by outgrowths of the posterior margin of the hypandrium (Figs 31-33, 53-54, *eds.*). The subgenital sclerite is situated between other structures of the male genitalia and the dorsal wall of the hypandrium (= dorsal sclerotisation of subgenital plate *sensu* Klass, 1997). Similar structures are present in some Ectobiidae (for instance, "ventral structure" in *Nahublattella* Bruijning, 1959; see Anisyutkin, 2009) and evidently belong to the labile complex of the male genital structures (see Anisyutkin, 2011). The structures of the labile complex do not belong to the groundplan of male genitalia, but most likely represent secondary sclerotizations of the intersternal membrane (Anisyutkin, 2011). These structures can appear "de novo" and the homologization of such secondary sclerites is very difficult. After preparation, the subgenital sclerite can be tightly pressed against the dorsal wall of the hypandrium

(Figs 31, 53, *sgs*.) or it can be separated along with other structures of the male genitalia (Figs 27, 40, 47, *sgs*.). This depends on the strength of the membranes and on the dissecting skills of the researcher.

Small rod-like sclerites located near the "folded sclerite" (Figs 34, 40, 47, 55, 63, *1.scl.*, *scl.*) belong to the labile complex or are rudiments of sclerites of the groundplan of the male genitalia.

The left dorsal phallomere (*ldp*.) and the left ventral phallomere (*lvp*.) (*sensu* Qiu *et al.*, 2017) form a single "folded sclerite" (Figs 27, 34, 40, 47, 55, 64-65, *f.scl*.).

The complete reduction of sclerite L3 (genital hook) is unusual but not unique for Corydiidae. The almost complete reduction of L3 was noted in representatives of the genus *Therea* Billberg, 1820 by Grandcolas (1993b).

Sexual dimorphism in the genus is variable. All males are fully winged (forma euptera). Qiu *et al.* (2017) report completely wingless females (forma aptera) of *Ctenoneura heixuanfeng* Qiu, Che & Wang, 2017 and suggested that all earlier records of fully winged females (Hanitsch, 1925; Bey-Bienko, 1957) should be considered as doubtful.

In this paper I follow Beccaloni (2014) and Qiu *et al.* (2019) who consider *Ctenoneura* as Corydiidae *incertae sedis*. Clarification of the phylogenetic position of the genus requires further research.

Species included: At present 39 species are known: *Ctenoneura annulicornis* Princis, 1954, *C. biguttata* Hanitsch, 1932, *C. birmanica* Princis, 1954, *C. brunnea* Hanitsch, 1929, *C. crassistyla* Roth, 1993, *C. fulva* Hanitsch, 1925, *C. gigantea* Roth, 1993, *C. hanitschi* Princis, 1954, *C. kemneri* Princis, 1967, *C. kinabaluana* Roth, 1993, *C. luma* Roth, 1993, *C. major* Hanitsch, 1925, *C. misera* Bey-Bienko, 1969, *C. mjoebergi* Princis, 1954, *C. murudensis* Roth, 1993, *C. parascutica* Roth, 1993, *C. poringa* Roth, 1993, *C. propannulicornis* Roth, 1993, *C. scutica* Roth, 1993, *C. simulans* Bey-Bienko, 1969, *C. sipitanga* Roth, 1995, *C. spinastyla* Roth, 1993, *C. triprocessa* Roth, 1993, *C. tuberculata* Princis, 1954, *C. uncata* Roth, 1993 and *C. yunnanea* Bey-Bienko, 1957 [as given in Beccaloni, 2014 with the exception of *Beybienkonus acuticerca* (Bey-Bienco, 1957)], *C. bawangensis* Qiu, Che & Wang, 2017, *C. delicata* Qiu, Che & Wang, 2017, *C. elongata* Qiu, Che & Wang, 2017, *C. heixuanfeng* Qiu, Che & Wang, 2017, *C. helicata* Qiu, Che & Wang, 2017, *C. papillaris* Qiu, Che & Wang, 2017, *C. qiuae* Qiu, Che & Wang, 2017, *C. complicata* sp. nov., *C. virgata* sp. nov., *C. asymmetrica* sp. nov., *C. emarginata* sp. nov., *C. orlovi* sp. nov. and *C. gorochovi* sp. nov.

Ctenoneura complicata sp. nov.

Figs 1-2, 13-27

Material examined: MHNG; male holotype (No. 160920/01); East Malaysia, Borneo, Sabah, Mt Kinabalu (Fig. 13A), 1500 m, sample no. 9; 30.IV.1987; leg. D. Burckhardt & I. Löbl.

Etymology: The Latin adjective "complicatus, -a, -um" refers to the complicated shape of the posterior margin of the hypandrium.

Description of male holotype: General body colour yellowish brown (Figs 1-2); head, central part of pronotum, part of thorax, coxae, femora and abdominal apex darker; eyes black. Surfaces dull and lustrous, punctuation absent. Head slightly longer than wide, globular, vertex slightly uneven, area between antennal sockets slightly protruded, with sutures running from antennal sutures to clypeus (Fig. 14); ocellar spots small but distinct; eyes large, distance between eyes about equal to eye length; distance between antennal sockets about equal to scape length (~0.3 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.2, 1.0, 1.8. Pronotum as in Fig. 15; anterior margin very weakly concave, nearly straight, posterior margin widely rounded. Tegmina and hind wings completely developed. Tegmina weakly sclerotized, translucent, venation partly reticulate and irregular (Fig. 20); *Sc* moderately thickened, with 1-3 anterior rami; *R* with 19-20 anterior and apical rami; intercalary vein present (Fig. 20, *i.v.*); *M* with 10-11 rami; *CuA* with 1 complete (reaching wing margin) or incomplete (not reaching wing margin) ramus; *CuP* thin, distinct, smoothly curved. Wings membranous, with exception of sclerotized area of anterior rami of *R* (Fig. 21); *Sc* simple; *RA* with about 11-13 anterior complete or incomplete rami; *M* with 4 rami; *CuA* pectinate, with 5-6 complete and 0-1 incomplete veins; a long and weak vein situated behind *CuA* (Fig. 21, *1pl.*), this probably corresponding to 1st plical vein *sensu* Rehn (1951) or to *CuP* [probably *CuP + A1 sensu* Bey-Bienko (1950)]; next vein not reaching wing margin and fused with previous one and with 1st anal vein (Fig. 21, *2pl.*), this probably corresponding to 2nd plical vein *sensu* Rehn (1951); 3rd vein weak and discernible only in proximal part (Fig. 21, *3pl.*), probably corresponding to 3rd plical vein *sensu* Rehn (1951); anal fan folded, consisting of 9 rami, first ramus proximally incrassated. Anterior margin of fore femora armed according to type C (*sensu* Bey-Bienko, 1950; Roth, 2003), with a single apical spine (Fig. 16). Fore tibiae not thickened distally; tibial spines weak (Figs 16-17). Structure of hind tarsi (Figs 18-19): metatarsus slightly longer than other segments combined; all euplantulae absent; spines along lower margins of tarsal segments arranged in single row; claws symmetrical, simple; arolium about half of claw length. Abdomen without visible glandular structure. Anal plate transverse (Fig. 22), with posterior margin medially protruded; dorsally with membranous spot. Paraprocts symmetrical, without armament, shaped like long trapezoid plates, with membranous pads at medial ends; *pv*-sclerites well developed (Fig. 23). Cerci with

Figs 1-12. *Ctenoneura* spp. Male holotypes. (1-2) *C. complicata* sp. nov. (3-4) *C. virgata* sp. nov. (5-6) *C. asymmetrica* sp. nov. (7-8) *C. emarginata* sp. nov. (9-10) *C. orlovi* sp. nov. (11-12). *C. gorochovi* sp. nov. (1, 3, 5, 7, 9, 11) Habitus, dorsal view. (2, 4, 6, 8, 10, 12) Habitus, ventral view. The black bars in Fig. 1 are insect pins fixing the specimen. Not to scale.

Fig. 13. Map of localities of *Ctenoneura* species described and discusses in this paper. (A) Borneo, Sabah, Mt Kinabalu: *C. complicata* sp. nov., *C. asymmetrica* sp. nov., *C. emarginata* sp. nov., *C. major*. (B) Peninsular Malaysia, Pahang, Cameron Highlands: *C. virgata* sp. nov. (C) Northern Vietnam, Lao Cai Prov., Sa Pa Distr., Mt Fan Si Pan: *C. orlovi* sp. nov. (D) Borneo, Sabah, Mt Trus Madi: *C. gorochovi* sp. nov. (E) Borneo, Sarawak, Mt Murud: *C. major*. (F) Southern Vietnam, Da Lat Plateau, Mt Lang Biang: *C. major*.

8 distinct segments (Fig. 22). Hypandrium broad and strongly asymmetrical (Figs 24-26); right anterolateral process larger than left one (Fig. 24); left posterolateral corner extended posteriorly, with small tooth at apex (Figs 24-26, *1st.pr.*); small and membranous left stylus situated medially (Fig. 24, *l.sty.*); 2 large curved outgrowths to their right (Figs 24-25, *2nd.pr.*, *3rd.pr.*); right posterolateral corner extended posterolaterally; between right large curved outgrowth and right posterolateral angle a small membranous outgrowth, probably the right stylus (Fig. 24, *r.sty.*); 3 complicated and strongly sclerotized outgrowths situated on posterodorsal side of hypandrium: the left one (Figs 25-26, *4.pr.*) dentate apically, the right one covered with long and curved bristles (Figs 25-26, *5.pr.*), cranial outgrowth shaped like a transverse plate, medially with thin curved process carrying a bristle (Figs 25-26, *6.pr.*). Male genitalia (Fig. 27): subgenital sclerite small and weakly sclerotized (Fig. 27, *sgs.*); "folded sclerite" (*ldp+lvp sensu* Qiu *et al.*, 2017) large and well sclerotized (Fig. 27, *f.scl.*); right phallomere with thin transverse sclerite (Fig. 27, *tvs.*).

Female: Unknown.

Measurements (in mm): Head length 1.3; head width 1.2; pronotum length 1.7; pronotum width 2.2; tegmen length 7.2; tegmen width 2.4.

Comparison: *Ctenoneura complicata* sp. nov. is somewhat similar to *C. yunnanea,* described from Yunnan, China (Bey-Bienko, 1957), in the presence of a rounded hollow on the posterior margin of the hypandrium, but both species clearly differ in general shape of the hypandrium (Fig. 24 cf. Bey-Bienko, 1957: fig. 1). The new species can be readily distinguished from all other congeners by the peculiar shape of its hypandrium, i.e. presence of two curved outgrowths on posterior margin and three complicated outgrowths situated on posterodorsal side of hypandrium (Figs 24-26). *Ctenoneura complicata* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and a posteriorly widely rounded and protruded pronotum (Fig. 15 cf. Roth, 1993: fig. 2A).

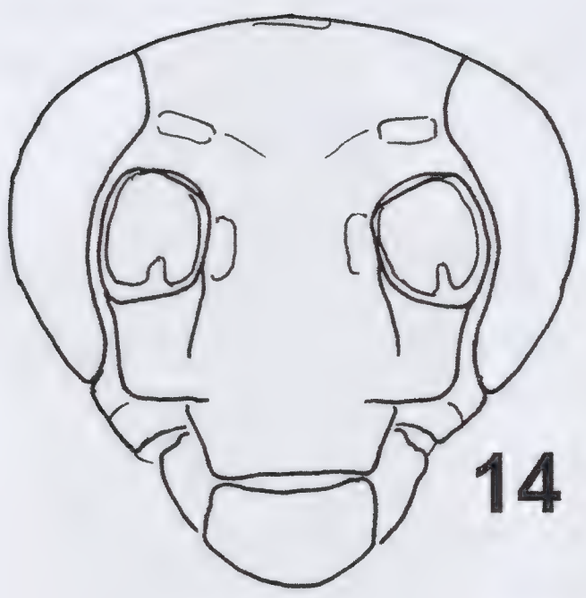
Ctenoneura virgata sp. nov.

Figs 3-4, 13, 28-34

Material examined: MHNG; male holotype (No. 160920/02); West Malaysia, Pahang, Cameron Highlands, Ringlet (Fig. 13B), 4200 feet; 7.VIII.1972; leg. T. Jaccoud.

Etymology: The Latin adjective "virgatus, -a, -um" (= shaped like a twigs or rod) refers to the peculiar structure of the subgenital sclerite.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but different in the following characters: Head with only one suture running from right antennal suture to clypeus (Fig. 28); distance between antennal sockets about 0.9 times scape length (~0.4 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.2, 1.0, 1.4. Tegmina and hind wing venation principally similar to that of *C. complicata* sp. nov.; tegmina with intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 30), mostly membranous (paraprocts clearly visible through anal plate; Fig. 30, *par.*), with posterior margin medially protruded. Hypandrium asymmetrical (Figs 31-33), with posterior margin folded up and roundly protruded medially; right posterolateral corner with folded-up outgrowth (Figs 32-33, *r.p.a.*) enclosing extended structure of subgenital sclerite (Figs 31-33, *eds.*); left stylus large (Figs 31-33, *l.sty.*), right one absent.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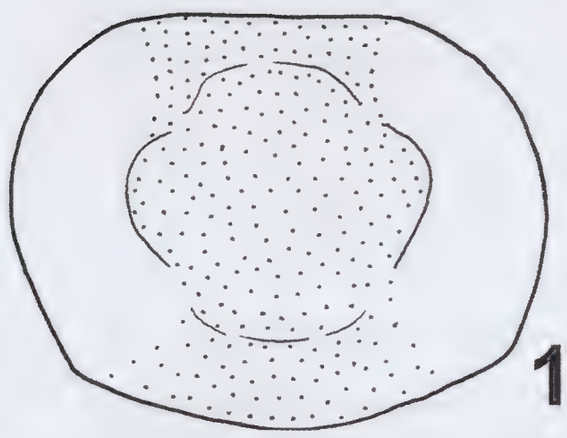
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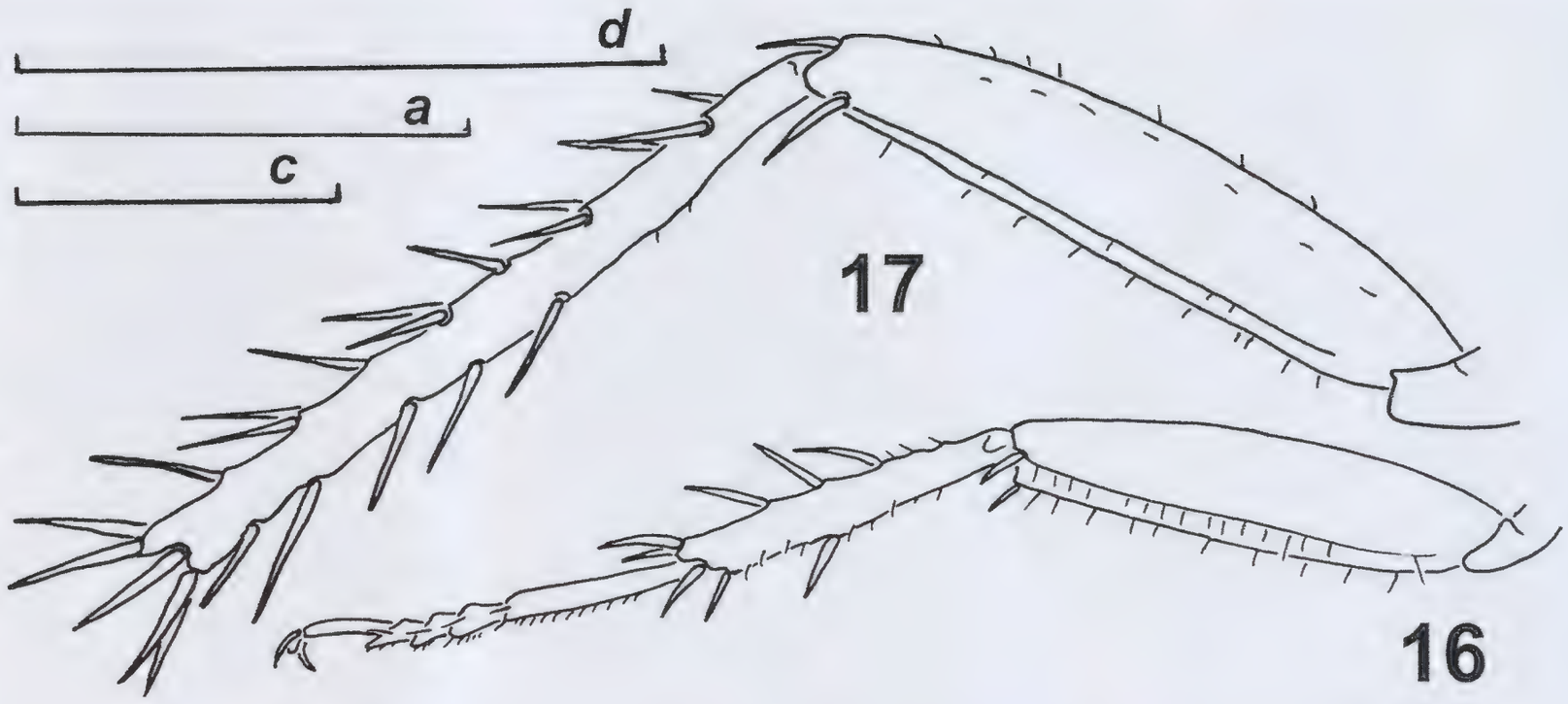

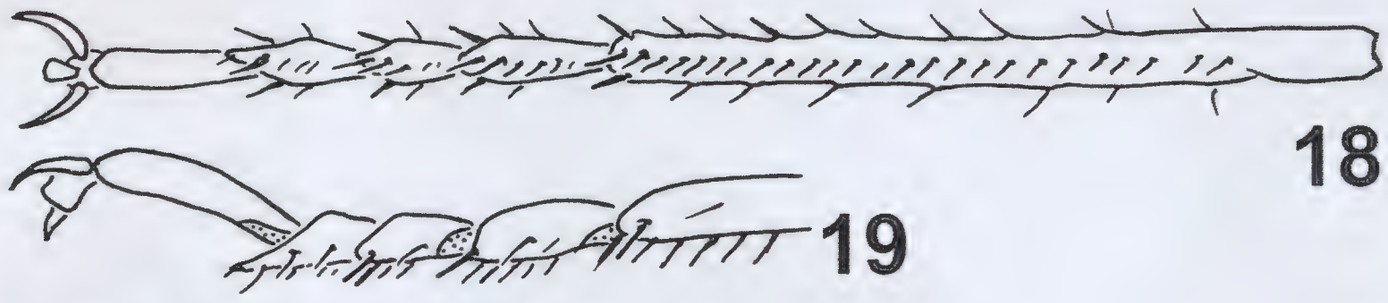

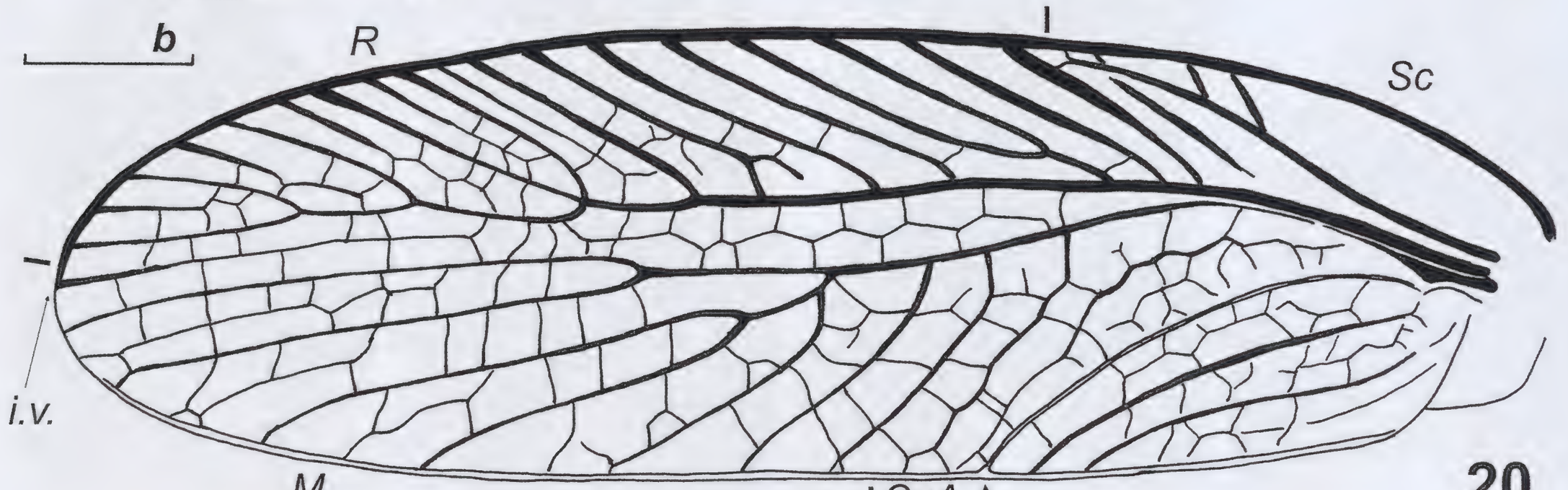

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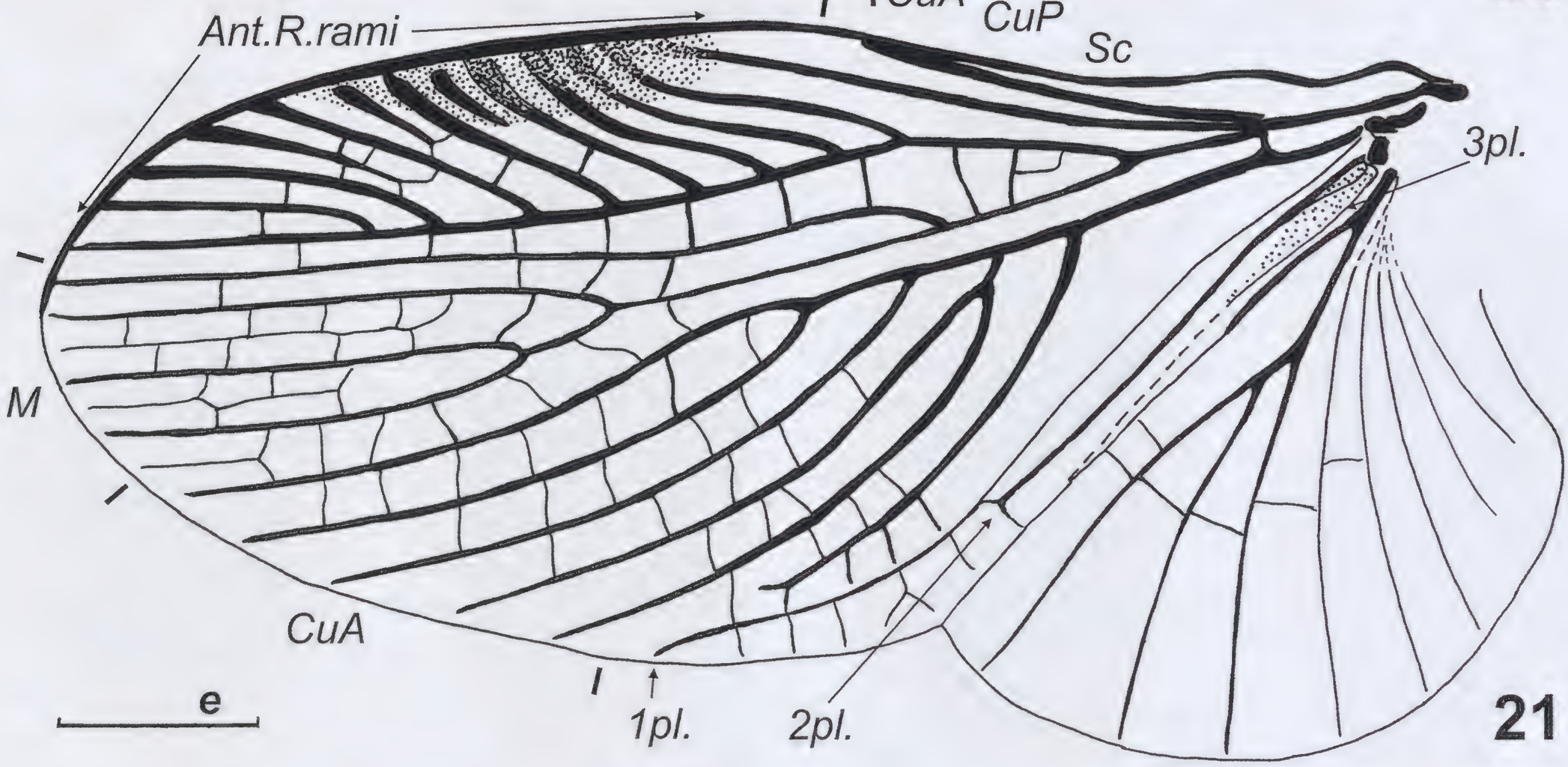

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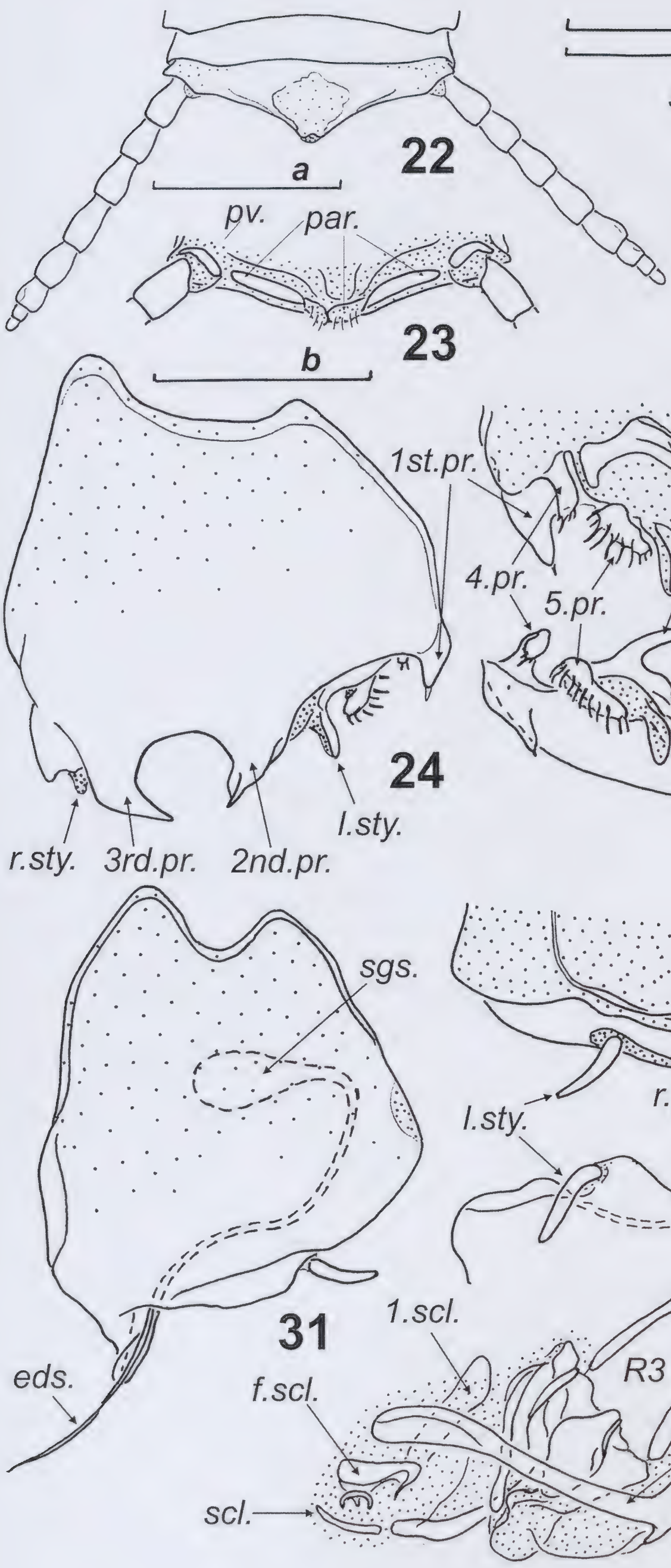
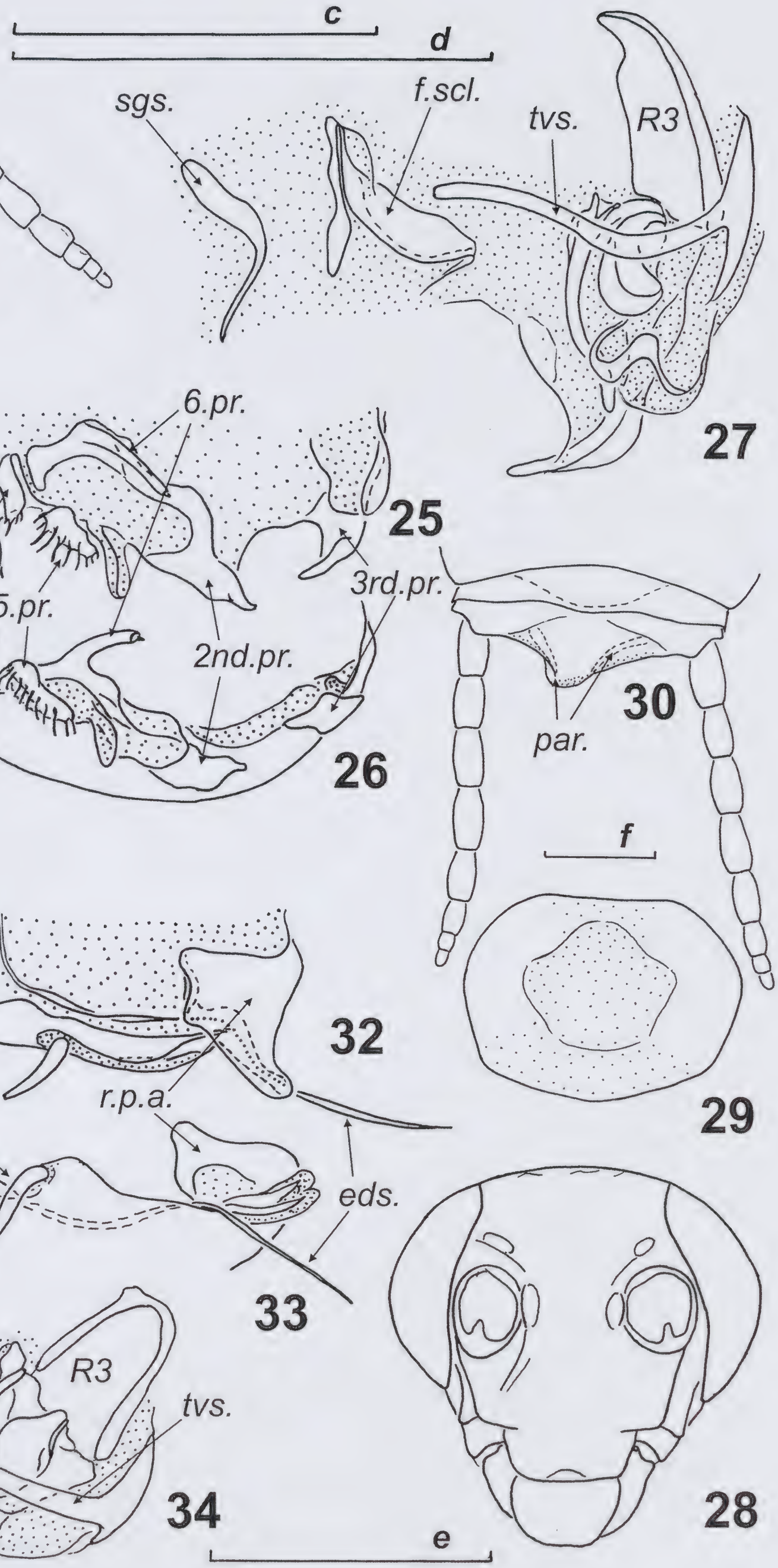
Figs 14-21. *Ctenoneura complicata* sp. nov., male holotype. (14) Facial part of head. (15) Pronotum, dorsal view. (16) Right fore leg, proventral view. (17) Right hind leg (tarsus not shown), proventral view. (18) Right hind tarsus, retroventral view. (19) Apical part of right hind tarsus, proventral view. (20) Left tegmen, dorsal view. (21) Left hind wing, dorsal view. Dotted areas indicate dark colour (15), sclerotized areas or strongly reduced part of 3rd plical vein (21). Abbreviations are explained in the paragraph "Material and methods". Scale bars 1 mm: a (14), b (15), c (16-17), d (18-19), e (20-21).





Figs 22-34. (22-27) *Ctenoneura complicata* sp. nov., male holotype (28-34) *C. virgata* sp. nov., male holotype. (22, 30) Abdominal apex, dorsal view. (23) Paraprocts and adjacent structures, ventral view. (24, 31) Hypandrium, ventral view. (25, 32) Posterior margin of hypandrium, dorsal view. (26, 33) Same, posterior view. (27, 34) Male genitalia, dorsal view. (28) Facial part of head. (29) Pronotum, dorsal view. Dotted areas indicate membranous parts (22-27, 30-34) or dark colour (29). Abbreviations are explained in "Material and methods". Scale bars 1 mm: a (22, 30), b (23), c (24-26, 31-33), d (27, 34), e (28), f (29).

Male genitalia (Figs 31-34): subgenital sclerite looped, large and well sclerotized (Fig. 31, *sgs*.), extending structure of subgenital sclerite long (Figs 31-33, *eds*.); "folded sclerite" (*ldp+lvp sensu* Qiu *et al*., 2017) small (Fig. 34, *f.scl.*); right phallomere with well sclerotized transverse sclerite (Fig. 34, *tvs*.); weakly sclerotized trapezoidal structure situated below "folded sclerite" (Fig. 34, *l.scl.*) and small rod-like sclerite situated near "folded sclerite" (Fig. 34, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.3; head width 1.2; pronotum length 1.8; pronotum width 2.5; tegmen length 8.4; tegmen width 2.4.

Comparison: The new species can be readily distinguished from all other congeners by the peculiar shape of its hypandrium, i.e. posterior margin folded up and protruded medially, right posterolateral corner with folded-up outgrowth (Figs 31-33). *Ctenoneura virgata* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and of a posteriorly rounded pronotum.

A similar switch-like extended structure of the subgenital sclerite is present in *C. orlovi* sp. nov. (see below) and *C. triprocessa* Roth, 1993, but these species can be readily distinguished by the structure of their hypandria (Fig. 31 cf. Roth, 1993: fig. 19A-E).

Remark: The asymmetrical suture running from the right antennal suture to the clypeus (Fig. 28) may be due to damage to the larva. To resolve the question of whether this character has a taxonomical value, it is necessary to examine additional material.

Ctenoneura asymmetrica sp. nov.

Figs 5-6, 13, 35-40

Material examined: MHNG; male holotype (No. 160920/03); East Malaysia, Borneo, Sabah, Mt Kinabalu National Park (Fig. 13A), 1500 m, collected by interception trap; 8.-16.V.1987; leg. A. Smetana.

Etymology: The Latin adjective "asymmetricus, -a, -um" (= asymmetrical) refers to the strongly asymmetrical shape of the hypandrium of this species.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but larger and darker, additionally different in the following characters: Head longer than wide, without sutures below antennal sockets (Fig. 35); distance between eyes about 0.9 times eye length; distance between antennal sockets about equal to scape length (~0.4 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.3, 1.0, 1.6. Pronotum as in Fig. 36. Tegmina and hind wing venation largely similar to that of *C. complicata* sp. nov.; tegmina with intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 37), dorsally with medial membranous spot. Cerci with 10 distinct segments, apical segment very small (Fig. 37). Hypandrium strongly asymmetrical (Figs 38-39); left posterolateral corner folded up (Fig. 39, *l.p.a.*); left stylus large (Figs 38-39, *l.sty.*); posterior margin medially emarginated; right posterolateral corner protruded into large and complicated outgrowth (Fig. 38, *r.p.a.*) with triangular outgrowth at outer side (Figs 38-39, *t.o.*), apically with distinct right stylus (Figs 38-39, *r.sty.*).

Male genitalia (Fig. 40): subgenital sclerite long and somewhat coiled (Fig. 40, *sgs*.); "folded sclerite" (*ldp+lvp sensu* Qiu *et al*., 2017) large and well sclerotized (Fig. 40, *f.scl.*); right phallomere with large and well sclerotized transverse sclerite (Fig. 40, *tvs*.); two small rod-like sclerites situated near "folded sclerite" (Fig. 40, *scl.*).

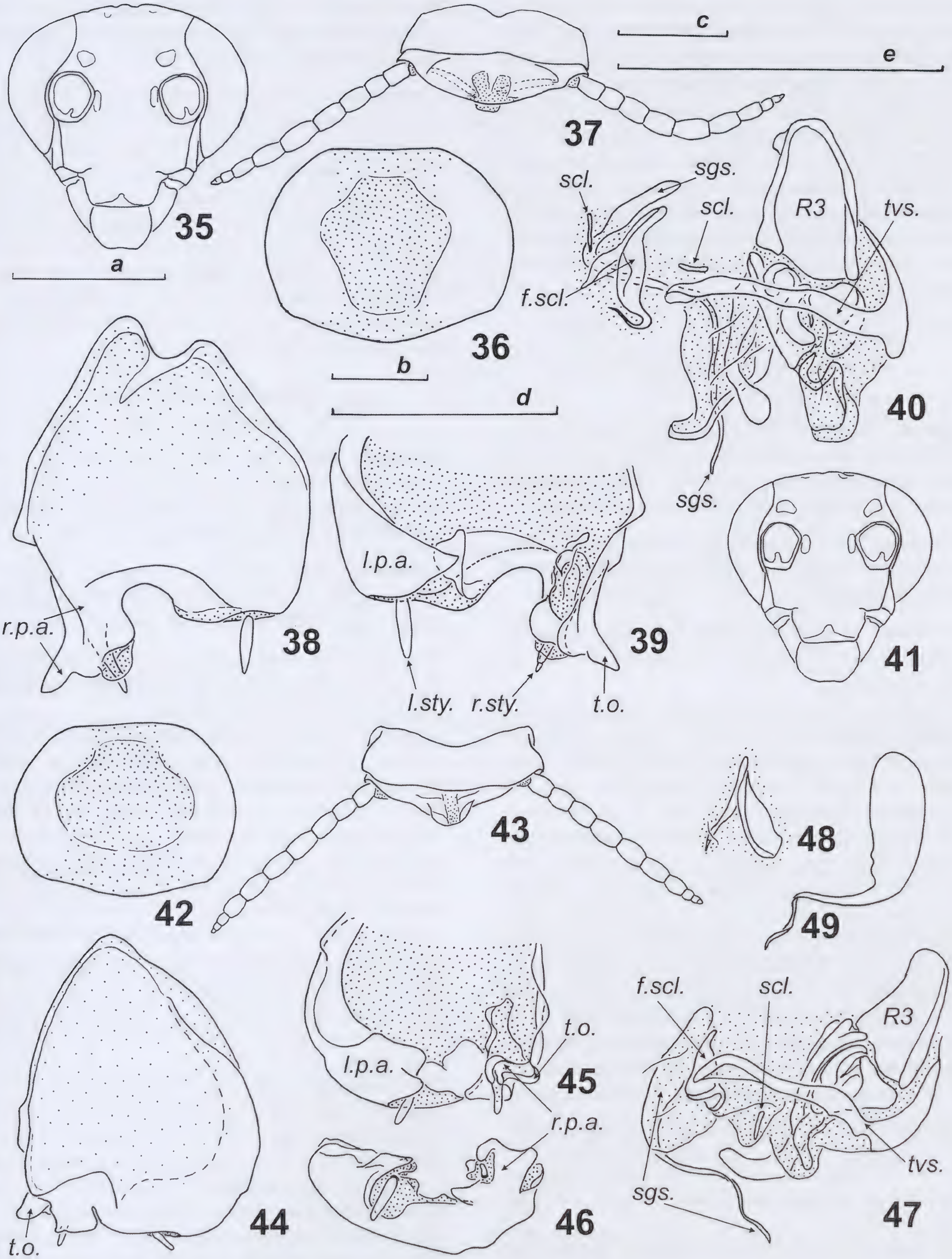
Female: Unknown.

Measurements (in mm): Head length 1.7; head width 1.4; pronotum length 2.0; pronotum width 2.6; tegmen length 9.8; tegmen width 2.9.

Comparison: The new species can be readily distinguished from all other congeners, with the exception of *C. major*, by the peculiar shape of its hypandrium, i.e. presence of a folded left posterolateral corner and of a large and complicated right outgrowth (Figs 38-39). *Ctenoneura asymmetrica* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and a posteriorly rounded pronotum.

Ctenoneura asymmetrica sp. nov. and *C. major* have a hypandrium of somewhat similar shape (Figs 38-39 cf. Roth, 1993: fig. 9D-E). The new species differs from *C. major* in the following characters: (1) interocular space wider than distance between ocellar spots, about equal to distance between antennal sockets (Fig. 35) (in *C. major* "interocular space less than distance between ocellar spots and antennal sockets"; see Roth, 1993: 96); (2) cerci with 10 segments (Fig. 37) (8 in *C. major*; see Hanitsch, 1925); (3) right posterolateral process of hypandrium with distinct, well sclerotized triangular outgrowth (Figs 38-39, *t.o.*) (in *C. major* outgrowth absent; Figs 38-39 cf. Roth, 1993: fig. 9D-E).

Remarks: *Ctenoneura major*, probably the species most closely related to *C. asymmetrica* sp. nov., was described from Mt Murud (Sarawak, Borneo) (Hanitsch, 1925) (Fig. 13E). Later this species was also discovered in Sabah (Mt Kinabalu; see Roth, 1995) (Fig. 13A) and in southern Vietnam, on the Da Lat Plateau [5500-7500 feet, Langbian Peaks (= Mt Lang Biang), S. Annam; see Hanitsch, 1927] (Fig. 13F). The most important



Figs 35-49. (35-40) *Ctenoneura asymmetrica* sp. nov., male holotype. (41-49) *C. emarginata* sp. nov., male holotype. (35, 41) Facial part of head. (36, 42) Pronotum, dorsal view. (37, 43) Abdominal apex, dorsal view. (38, 44) Hypandrium, ventral view. (39, 45) Posterior margin of hypandrium, dorsal view. (46) Same, posterior view. (40, 47) Male genitalia, dorsal view. (48) "Folded sclerite" of male genitalia. (49) Subgenital sclerite of male genitalia, ventral view. Dotted areas indicate dark colour (36, 42) or membranous parts (37-40, 43-48). Abbreviations are explained in "Material and Methods". Scale bars 1 mm: a (35, 41), b (36, 42), c (37, 43), d (38-39, 44-46), e (40, 47-49).

characters for species determination in *Ctenoneura* are characters of the hypandrium. Hanitsch (1925, 1927) described species mainly on the base of tegmina and wing venation, paying little attention to the structure of the hypandrium. In the original description of *C. major* characters of the hypandrium are not mentioned at all (Hanitsch, 1925). Taking this into account, the record from southern Vietnam needs confirmation. However, a similar range, including Sabah and southern Vietnam, is known, for example, for the praying mantis *Ceratocrania macra* Westwood, 1889 (Shcherbakov & Anisyutkin, 2018).

Ctenoneura emarginata sp. nov.

Figs 7-8, 13, 41-49

Material examined: MHNG; male holotype (No. 160920/04); East Malaysia, Borneo, Sabah, Mt Kinabalu National Park (Fig. 13A), 1500 m, collected by interception trap; 25.-30.IV.1987; leg. A. Smetana.

Etymology: The Latin adjective "emarginatus, -a, -um" (= notched) refers to the shape of posterior margin of the hypandrium.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but different in the following characters.

Head without sutures below antennal sockets (Fig. 41); distance between eyes about 0.9 times eye length; distance between antennal sockets about equal to scape length (~0.4 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.2, 1.0, 1.6. Pronotum as in Fig. 42. Tegmina and hind wing venation largely similar to those of *C. complicata* sp. nov.; tegmina with very short intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 43), well sclerotized, with only a longitudinal stripe of weak sclerotization, its posterior margin medially rounded and protruded. Cerci with 10 distinct segments, apical segment very small (Fig. 43). Hypandrium asymmetrical (Figs 44-46); left and right anterolateral processes fused; left posterolateral corner folded up, bifurcated apically (Fig. 45, *l.p.a.*); posterior margin medially rounded, with deep and narrow notch; right posterolateral corner of complicated shape (Figs 45-46, *r.p.a.*), with a triangular outgrowth on its outer side (Figs 44-45, *t.o.*); left and right syli distinct.

Male genitalia (Figs 47-49): subgenital sclerite long and slightly coiled (Figs 47, 49, *sgs.*); "folded sclerite" (*f.scl.*, corresponding to *ldp+lvp* of Qiu *et al.*, 2017) as in Figs 47-48; right phallomere with distinct transverse sclerite (Fig. 47, *tvs.*); small rod-like sclerite situated near "folded sclerite" (Fig. 47, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.4; head width 1.3; pronotum length 1.8; pronotum width 2.3; tegmen length 8.9; tegmen width 3.2.

Comparison: *Ctenoneura emarginata* sp. nov. can be readily distinguished from all other congeners by the shape of its hypandrium, i.e. left posterolateral corner folded up and bifurcated apically, posterior margin of hypandrium deeply notched, right posterolateral corner complicated, with outer triangular outgrowth (Figs 44-46). The new species differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and a posteriorly rounded pronotum (see Fig. 42 and Roth, 1993: fig. 2A).

Ctenoneura orlovi sp. nov.

Figs 9-10, 13, 50-55

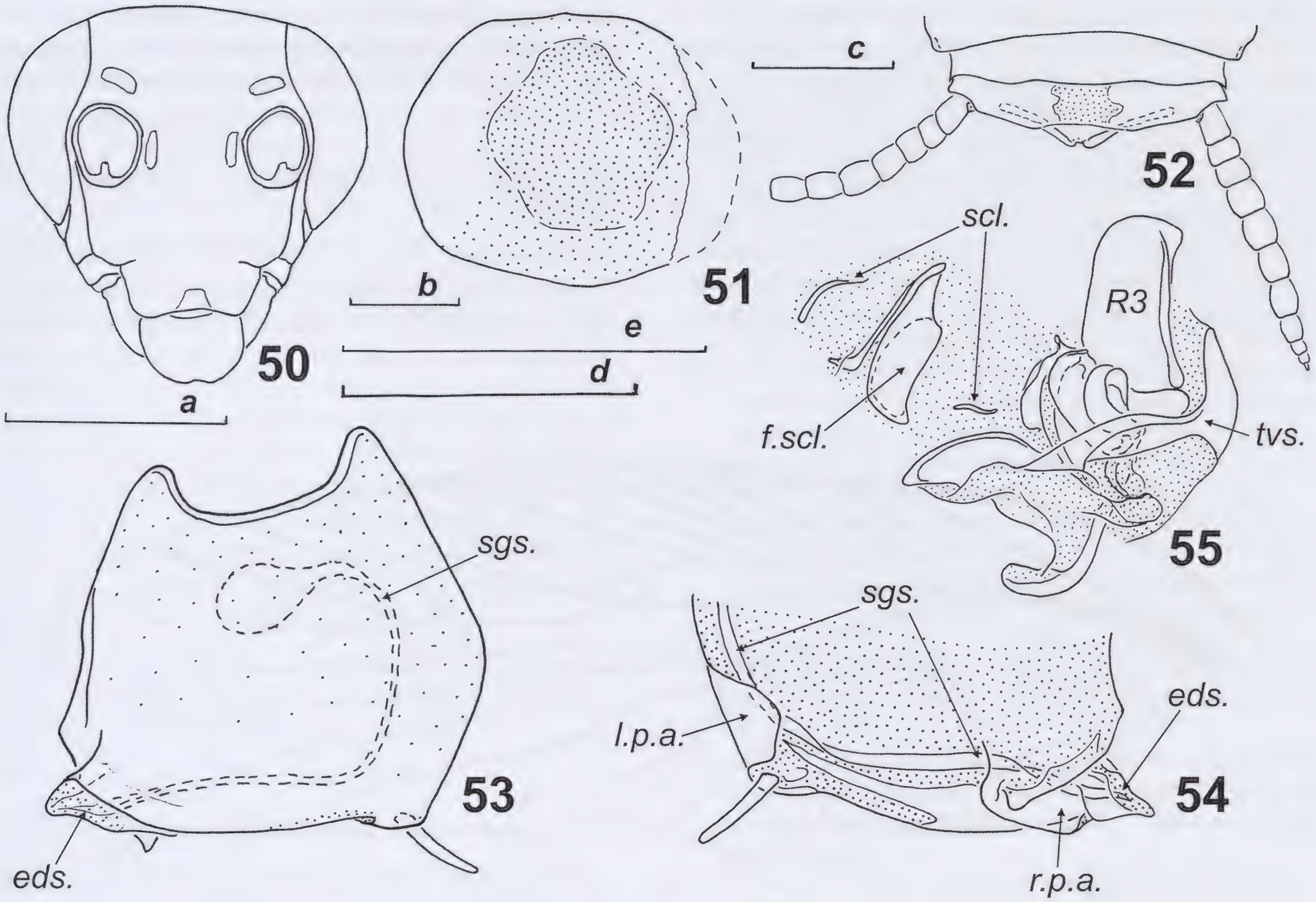
Material examined: ZIN; male holotype (No. 160920/05); Vietnam, Lao Cai Prov., Sa Pa Distr., Mt Fan Si Pan (Fig. 13C), 1400-1500 m, 22°8'56"N, 103°49'35"E; 26.V.-6.VI.1999; leg. N.L. Orlov.

Etymology: This species is named in honour of the collector of the holotype, the famous Russian herpetologist Dr Nikolai L. Orlov.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but larger, additionally different in the following characters.

Head without sutures below antennal sockets (Fig. 50); distance between eyes about equal to eye length; distance between antennal sockets about equal to scape length (~0.5 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.4, 1.0, 1.5. Pronotum as in Fig. 51, anterior margin very weakly protruded; right paranotalium broken off. Tegmina and hind wing venation largely similar to those of *C. complicata* sp. nov.; tegmina with a very short intercalary vein; hind wings with strongly sclerotized area of anterior rami of *R*, in this area veins indiscernible. Anal plate transverse (Fig. 52), its posterior margin medially protruded and separated by a transverse fold; dorsally with a membranous spot. Right cercus with 11 distinct segments, the apical one very small; left cercus partly broken off, with 7 basal segments remaining (Fig. 52). Hypandrium broad and asymmetrical (Figs 53-54); left anterolateral process larger than right one; left posterolateral corner folded up (Fig. 54, *l.p.a.*), posterior margin widely rounded; right posterolateral corner of complicated shape (Fig. 54, *r.p.a.*), with an outgrowth directed postero-dorsal, this outgrowth forming fold and supporting extended structure of subgenital sclerite (Figs 53-54, *eds.*); left stylus large, right one absent.

Male genitalia (Figs 53-55): subgenital sclerite long and strongly curved (Figs 53-54, *sgs.*); "folded sclerite" (corresponding to *ldp+lvp* of Qiu *et al.*, 2017) large and well sclerotized (Fig. 55, *f.scl.*); right phallomere with



Figs 50-55. *Ctenoneura orlovi* sp. nov., male holotype. (50) Facial part of head. (51) Pronotum, dorsal view. (52) Abdominal apex, dorsal view. (53) Hypandrium, ventral view. (54) Posterior margin of hypandrium, dorsal view. (55) Male genitalia, dorsal view. Dotted areas indicate dark colour (51) or membranous parts (52-55). Abbreviations are explained in "Material and Methods". Scale bars 1 mm: a (50), b (51), c (52), d (53-54), e (55).

wide transverse sclerite (Fig. 55, *tvs.*); two small rod-like sclerite located near "folded sclerite" (Fig. 55, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.7; head width 1.6; pronotum length 2.5; pronotum width ~3.0 (right paranotalium broken off); tegmen length 10.2; tegmen width 3.1.

Comparison: The new species can be readily distinguished from all other congeners by the peculiar shape of its hypandrium, i.e. presence of a folded up left posterolateral corner, widely rounded posterior margin, complicated outgrowth at right posterolateral corner and large left stylus (Figs 53-54). *Ctenoneura orlovi* sp. nov. differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by the presence of an intercalary vein and an angular, protruded posterior margin of the pronotum.

Ctenoneura gorochovi sp. nov.

Figs 11-13, 56-65

Material examined: ZIN; male holotype (No. 160920/06); East Malaysia, Sabah, Mt Trus Madi (Fig. 13D), about 1000 m, partly primary / partly secondary forest; 13.-25.V.2007; leg. A.V. Gorochov.

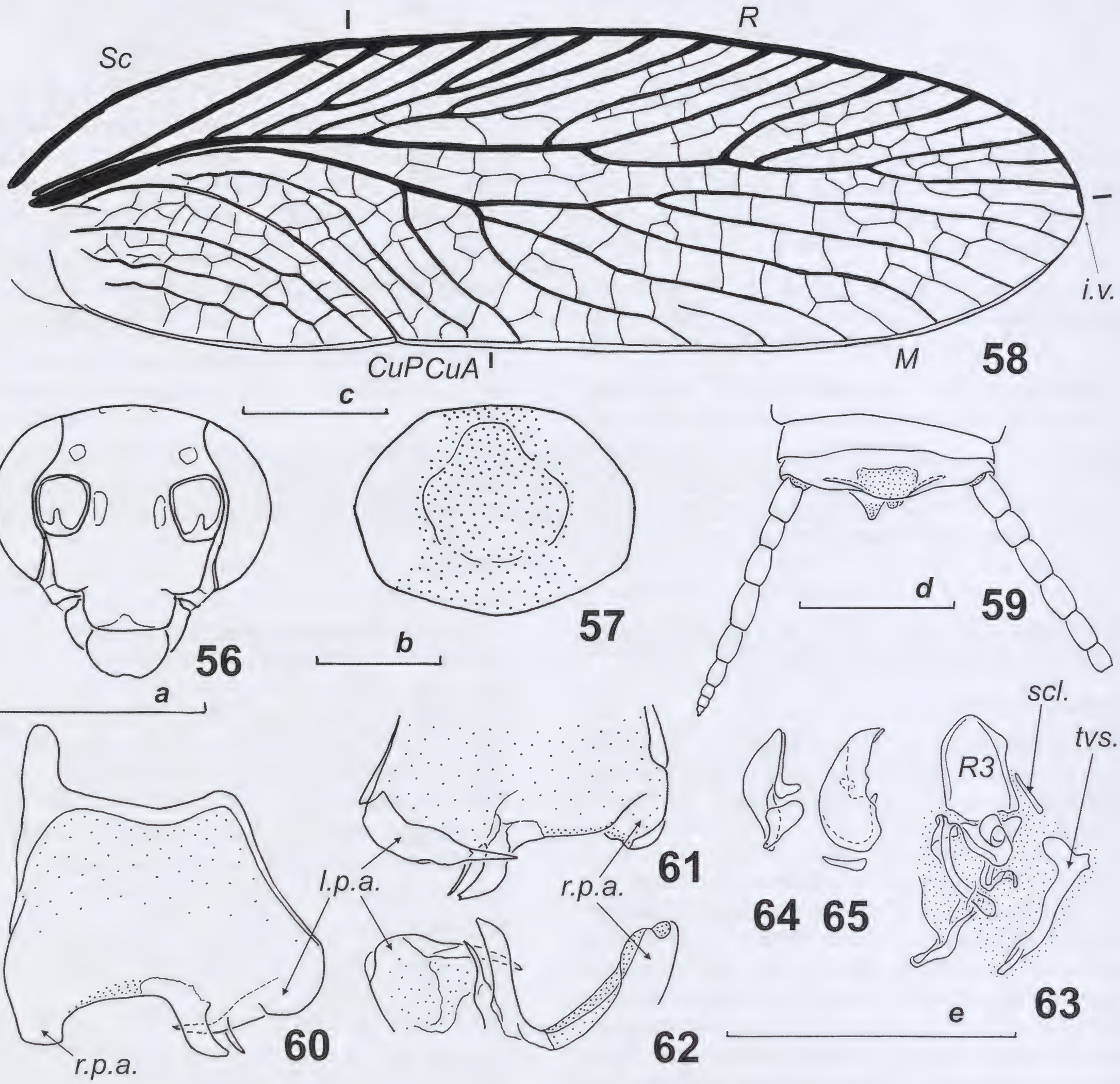
Etymology: This species is named in honour of the collector of the holotype, the famous Russian orthopterologist Dr Andrey V. Gorochov.

Description of male holotype: Generally similar to *Ctenoneura complicata* sp. nov., but different in the following characters.

Head about as long as wide, without sutures below antennal sockets (Fig. 56); distance between eyes about equal to eye length; distance between antennal sockets about equal to scape length (~0.3 mm); approximate length ratio of 3rd to 5th segments of maxillary palps 1.4, 1.0, 1.3. Pronotum as in Fig. 57. Tegmina and hind wing venation largely similar to those of *C. complicata* sp. nov.; tegmina with very short intercalary vein (Fig. 58, *i.v.*); hind wings with moderately sclerotized area of

anterior rami of *R*, in this area veins almost indiscernible. Anal plate transverse (Fig. 59), its posterior margin medially protruded and separated by transverse fold; dorsally with a membranous spot. Left cercus with 9 distinct segments, the apical one very small, with attenuate apex; the right cercus partly broken off, with 6 basal segments remaining (Fig. 59). Hypandrium broad (Figs 60-62); right anterolateral process larger than left one; left posterolateral corner drawn out into mediad-directed spine (Figs 60-62, *l.p.a.*); strongly sclerotized tooth-like process situated near middle of posterior margin of hypandrium; a small sclerotized spine to the left of tooth-like process; a wide and rounded notch with weakly sclerotized edges situated to the right of these spines; right posterolateral corner in the shape of an obtuse unarmed outgrowth (Figs 60-62, *r.p.a.*); styli absent.

Male genitalia (Figs 63-65): subgenital sclerite absent; "folded sclerite" (corresponding to *ldp+lvp* of Qiu *et al*., 2017) well sclerotized (Figs 64-65); right phallomere



Figs 56-65. *Ctenoneura gorochovi* sp. nov., male holotype. (56) Facial part of head. (57) Pronotum, dorsal view. (58) Right tegmen, dorsal view. (59) Abdominal apex, dorsal view. (60) Hypandrium, ventral view. (61) Posterior margin of hypandrium, dorsal view. (62) Same, posterior view. (63) Right phallomere of male genitalia, dorsal view; structures partly disarticulated. (64) "Folded sclerite" of male genitalia. (65) Same at different angle of view plus small accessory sclerite. Dotted areas indicate dark colour (57) or membranous parts (59-63). Abbreviations are explained in "Material and methods". Scale bars 1 mm: a (56), b (57), c (58), d (59), e (60-65).

with well sclerotized transverse sclerite (Fig. 63, *tvs.*); two small rod-like sclerites situated near "folded sclerite" (Fig. 65) and near right phallomere (Fig. 63, *scl.*).

Female: Unknown.

Measurements (in mm): Head length 1.2; head width 1.2; pronotum length 1.7; pronotum width 2.2; tegmen length 7.4; tegmen width 2.3.

Comparison: *Ctenoneura gorochovi* sp. nov. can be readily distinguished from all other congeners by the shape of its hypandrium, i.e. mediad-directed spine present at posterolateral corner, tooth-like process situated near middle, posterior margin of hypandrium with wide and rounded notch, styli absent (Figs 60-62). The new species differs from *C. gigantea* (known only from a single specimen with missing abdomen; see Roth, 1993) by smaller size and by the presence of an intercalary vein and a posteriorly rounded pronotum (see Fig. 57 and Roth, 1993: fig. 2A).

Remark: The abdomen of the holotype is damaged (Fig. 12) and therefore the genitalia sclerites are distorted and disarticulated (Figs 63-65).

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REFERENCES

Andersen T., Kjaerandsen J. 1995. Three new species of *Nocticola* Bolívar from Ghana, West Africa (Blattaria: Nocticolidae). *Journal of African Zoology* 109(4): 377-385.

Anisyutkin L.N. 2009. New representatives of the genus *Nahublattella* Bruijning, 1959 (Dictyoptera, Blattellidae) from Central and South America. *Entomological Review* 89(7): 820-838. DOI: 10.1134/s0013873809070082

Anisyutkin L.N. 2011. A review of the genus *Euphyllodromia* Shelford, 1908 (Dictyoptera: Ectobiidae), with description of three new species. *Proceedings of the Zoological Institute RAS* 315(4): 369-398.

Anisyutkin L.N. 2014. New and little known Blattidae (Dictyoptera) from the collection of the Muséum d'histoire naturelle de Genève. *Revue suisse de Zoologie* 121(1): 33-50.

Anisyutkin L.N., Telnov D. 2018. New data on the cockroaches previously attributed to the genus *Duchailluia* Rehn, 1933 (Dictyoptera: Blattidae: Blattinae). *Zootaxa* 4532(4): 523-538. DOI: 10.11646/zootaxa.4532.4.4

Anisyutkin L.N., Anichkin A.E., Nguyen V.T. 2013. *Macrostylopyga* gen. nov., a new genus of cockroaches (Dictyoptera: Blattidae), with description of two new species. *Zootaxa* 3635(5): 520-532. DOI: 10.11646/zootaxa.3635.5.2

Beccaloni G.W. 2014. Cockroach species file online. Version 5.0/5.0. Available at http://Cockroach.SpeciesFile.org (accessed July 21, 2021).

Bey-Bienko G.Y. 1950. Cockroach insects. *Fauna of USSR* (N.S.) 40: 1-343.

Bey-Bienko G.Y. 1957. The results of the Chinese-Soviet zoologico-botanical expeditions to southwestern China 1955-1956. *Entomologicheskoe Obozrenie* 36(4): 895-915.

Bey-Bienko G.Y. 1969. New genera and species of cockroaches (Blattoptera) from tropical and subtropical Asia. *Entomologicheskoe Obozrenie* 48(4): 831-862.

Billberg G.J. 1820. Enumeratio insectorum in Museo Gustave Johann Billberg. *Typis Gadelianis, Stockholm*, 138 pp.

Bolivar I. 1892. Orthoptères (pp. 29-34). *In*: Raffray A., Bolivar I., Simon E., Voyage de M.E. Simon aux Îles Philippines (Mars et Avril 1890). Etude sur les Arthropodes cavernicoles de l'île de Luzon. *Annales de la Société Entomologique de France* 61, 524 pp.

Brullé M.A. 1835. Orthoptères (pp. 1-415). *In*: Audouin M.V. (ed.), Histoire Naturelle des Insectes, 9. *Moessard, Paris*, 415 pp.

Bruijning C.F.A. 1959. The Blattidae of Surinam (pp. 1-103). *In*: Geijskes D.C., Hummelinck P.W. (eds), Studies on the fauna of Suriname and other Guyanas, 2. *Martinus Nijhoff, The Hague*, 103 pp.

Burmeister H. 1838. Handbuch der Entomologie, Band 2, Abteilung 2. *Guslin., Berlin*, pp. 397-1050.

Grandcolas P. 1993a. La position phylogénétique de *Miroblatta* Shelford, 1906 et l'évolution de la plicature des ailes chez les blattes (Dictyoptera: Blattaria). *Annales de la Société entomologique de France* (N.S.) 29(4): 345-349.

Grandcolas P. 1993b. Le genre *Therea* Billberg, 1820: position phylogénétique, nouvelles espèces, répartition, valence écologique (Dictyoptera, Blattaria, Polyphaginae). *Canadian Journal of Zoology* 71: 1816-1822. DOI: 10.1139/z93-259

Hanitsch R. 1925. On a collection of Blattidae from northern Sarawak, chiefly Mt. Murud and Mt. Dulit. *Sarawak Museum Journal* 3(1): 75-106.

Hanitsch R. 1927. On a collection of Blattidae from southern Annam. *Journal of the Siam Society, Natural History* Supplement 7(1): 7-48.

Hanitsch R. 1929. Fauna Sumatrensis. Beitrag No. 63. Blattidae. *Tijdschrift voor Entomologie* 72: 263-302.

Hanitsch R. 1932. On a collection of blattids from the east coast of Sumatra. *Miscellanea Zoologica Sumatrana* 62: 1-8.

Klass K.-D. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonner Zoologische Monographien* 42: 1-341.

Princis K. 1950. Entomological results from the Swedish expedition 1934 to Burma and British India. *Arkiv för Zoologi* 1(16): 203-222.

Princis K. 1954 (for 1953). Kleine Beiträge zur Kenntnis der Blattarien und ihrer Verbreitung. VI. *Entomologisk Tidskrift* 74(4): 203-213.

Princis K. 1967. Kleine Beiträge zur Kenntnis der Blattarien und ihrer Verbreitung. X. *Opuscula Entomologica* 32: 141-151.

Qiu L., Che Y.-L., Wang Z.-Q. 2017. Contribution to the

cockroach genus *Ctenoneura* Hanitsch, 1925 (Blattodea: Corydioidea: Corydiidae) with descriptions of seven new species from China. *Zootaxa* 4237(2): 265-299. DOI: 10.11646/zootaxa.4237.2.3

Qiu L., Yang Z.-B., Wang Z.-Q., Che Y.-L. 2019. Notes on some corydiid species from China, with description of a new genus (Blattodea: Corydioidea: Corydiidae). *Annales de la Société entomologique de France* (N.S.) 55(3): 261-273. DOI: 10.1080/00379271.2019.1603081

Rehn J.A.G. 1933 (for 1932). African and Malagasy Blattidae (Orthoptera). Part II. *Proceedings of the Academy of Natural Sciences of Philadelphia* 84: 405-511.

Rehn J.W.H. 1951. Classification of the Blattaria as indicated by their wings (Orthoptera). *Memoirs of the American Entomological Society* 14: 1-134.

Roth L.M. 1993. Revision of the cockroach genus *Ctenoneura* Hanitsch (Blattaria, Polyphagidae). *Tijdschrift voor Entomologie* 136: 83-109.

Roth L.M. 1995. Description of a new species of *Ctenoneura* Hanitsch from Sabah (Blattaria, Polyphagidae). *Tijdschrift voor Entomologie* 138: 117-119.

Roth L.M. 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Oriental Insects* 37: 1-186. DOI: 10.1080/00305316.2003.10417344

Shcherbakov E., Anisyutkin L.N. 2018. Update on the praying mantises (Insecta: Mantodea) of South-East Vietnam. *Annales de la Société entomologique de France* (N.S.) 54(2): 119-140. DOI: 10.1080/00379271.2018.1447394

Shelford R. 1906. Studies of the Blattidae. III. Some new Blattidae from Sarawak, Borneo in the Hope Department, Oxford University Museum. *Transactions of the Entomological Society of London* 54: 265-278.

Walker F. 1869. Catalogue of the specimens of Dermaptera, Saltatoria and supplement to the Blattariae in the collection of the British Museum. *British Museum, London*, 224 pp.

Westwood J.O. 1889. Revisio insectorum familiae mantidarum, speciebus novis aut minus cognitis descriptis et delineatis. *Gurney & Jackson, London*, iii + 53 pp.

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Two new species of Cestoda (Cyclophyllidea: Dilepididae) from Ploceidae and Passeridae (Aves: Passeriformes) in Côte d'Ivoire

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Abstract: Two new dilepidid cestodes parasitic in common landbirds of Ivory Coast are described. *Spiniglans thomassankara* sp. nov. was found in *Ploceus nigerrimus castaneofuscus* (Ploceidae) and other *Ploceus* species along the lagoon system of the South East of the country. It shows characters similar to those of members of both *Spiniglans* and *Dictymetra* but lacks a clearly visible ductus masculinus. It is characterized by 24-26 comparatively long hooks and a massive ovary. *Monopylidium comoensis* sp. nov. was found in *Gymnoris dentata* (Passeridae) in the Sudanian savanna from the North Eastern corner of the country. It shows 20-22 hooks 13.5-16.5 long, 14-25 testes and a distally enlarged vagina. The unknown parasites richness of very common hosts is underscored.

Keywords: Parasites - tapeworms - *Spiniglans* - *Monopylidium* - bird hosts - West Africa - non-model organisms.

INTRODUCTION

The cestode fauna of birds of the République de Côte d'Ivoire (Ivory Coast, West Africa) is one of the better known of the continent (Mariaux, 1994), even if only a small proportion of the country's global avian diversity of 745 species (Lepage, 2021) has been examined (Mariaux, 1994; Georgiev & Mariaux, 2007, and references therein). An abundant additional material collected in the last 40 years and kept in the Natural History Museum of Geneva remains to be studied in detail. Here, I report on two new dilepidid species parasitic in granivorous passerines in the genera *Ploceus* and *Gymnoris*.

MATERIAL AND METHODS

Birds were collected using mist nets in 1985, 1987, and 1988 by the author, and in 2010 by V. Widmer and M. E. Konan, from various localities in South Eastern Côte d'Ivoire along lagoons lining the Atlantic Coast and around the Ouango Fitini abandoned field station in the North East of the country. Hosts were sorted at mist net side, transported to the lab in fabric bags and euthanized as soon as possible with an excess of chloroform. Dissections, fixation and staining were performed according to standard procedures (see e.g. Mariaux & Georgiev, 2020), and stained specimens were mounted in Canada balsam. Some scoleces were squashed in Berlese's medium to facilitate examination of rostellar hooks.

All measurements are given in micrometers (if not indicated otherwise) as the range, with the mean and the number (n) of measurements or counts in parentheses. These are followed by values for holotype within square brackets where available. All specimens are deposited in the Helminthological Collections of the Museum of Natural History (MHNG-PLAT) in Geneva, Switzerland. Some of the hosts are also deposited in the same Institution with numbers from its bird collection (MHNG-OIS).

TAXONOMIC PART

Spiniglans thomassankara sp. nov.

Figs 1-5

Holotype: MHNG-PLAT-0015962 (formerly MHNG 988.402); Côte d'Ivoire, District Autonome d'Abidjan, Songon, fields ab. 7 km E of Dabou; WGS84 5.33, -4.31, 3 m; 21.04.1988. From *Ploceus nigerrimus castaneofuscus* (Lesson, 1840) (Passeriformes, Ploceidae); MHNG-OIS-1774.026.

Paratype: MHNG-PLAT-0015941 (formerly MHNG 985.637); 1 specimen; Côte d'Ivoire, District Autonome d'Abidjan, Adiopodioumé, former Orstom Experimental Fields; WGS84 5.33, -4.14, 45 m; 24.10.1985. From

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Ploceus nigerrimus castaneofuscus (Passeriformes, Ploceidae); MHNG-OIS-1774.014.

Other material:

- From *Ploceus nigerrimus castaneofuscus*
  MHNG-PLAT-0137397-8, MHNG-PLAT-0137400-1; 4 specimens; Côte d'Ivoire, Comoé, Nouamou, along Western end of Ehy Laguna; WGS84 5.18, -2.90, 17 m; 03.06.2010-06.06.2010. MHNG-OIS-1982.041-2, MHNG-OIS-1982.046.
- From *Ploceus cucullatus* (Statius Muller, 1776)
  MHNG-PLAT-0137402; 3 specimens. Same locality as paratypes. 09.06.2010.
- From *Ploceus nigricollis brachypterus* Swainson, 1837.
  MHNG-PLAT-0015956 (formerly MHNG 987.290); 2 specimens. Same locality as paratypes. 27.04.1987. MHNG-OIS-1774.050.
- From *Ploceus* sp.
  MHNG-PLAT-0015951 (formerly MHNG 985.636); 1 specimen. Same locality as paratypes; 23.07.1985.

Comparison material studied: MHNG-PLAT-0040450, 5 slides. *Spiniglans microsoma* (Southwell, 1922), "cotypes".

Prevalences: 7/36 (19%) in *P. nigerrimus*; 1/16 (6%) in *P. nigricollis*; 1/42 (2%) in *P. cucullatus.*

Intensity: 1-3.

Etymology: The specific epithet (a noun in apposition) honours, and is dedicated to, Thomas Isidore Noël Sankara (1949-1987), former president of the Burkina Faso, who was enlightening the West Africa subregion when these specimens were collected.

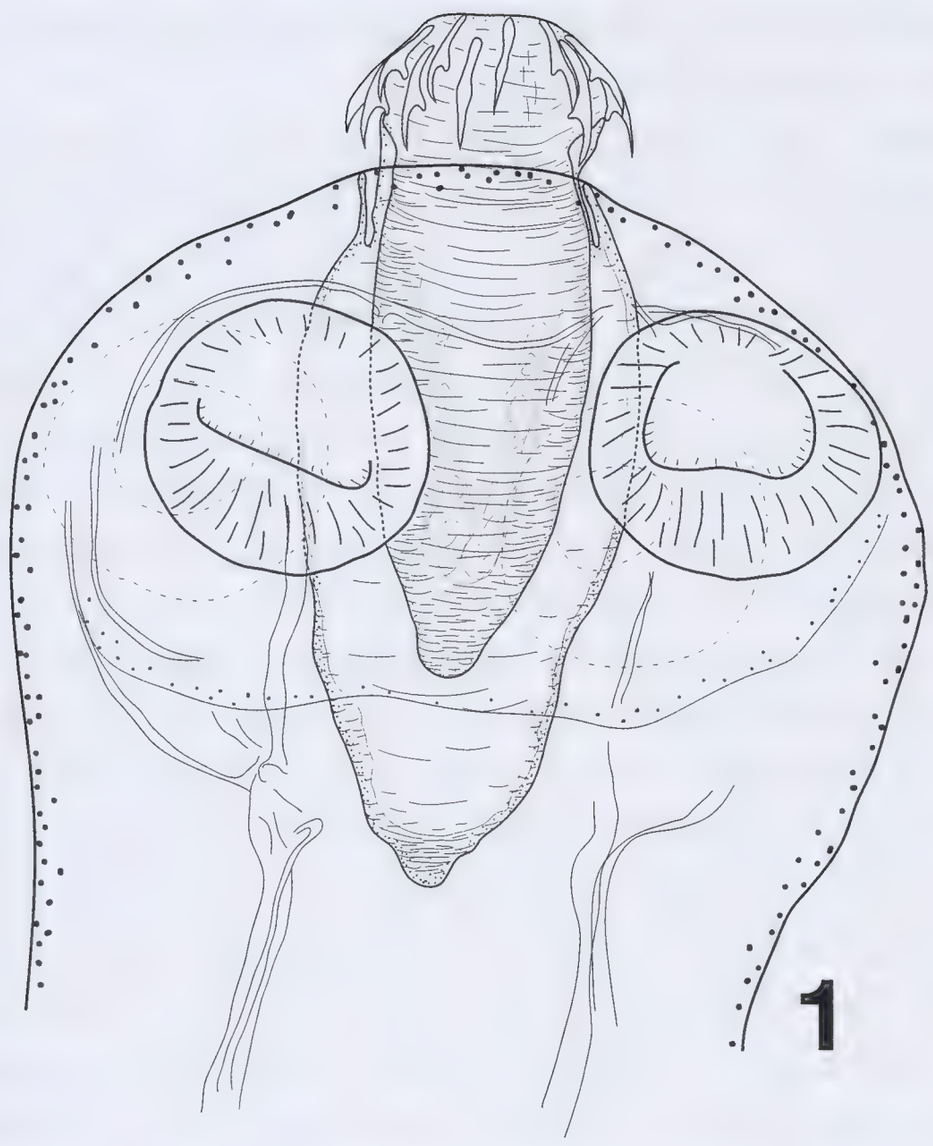
Description: Worm with body of medium size, up to 78 mm in length and with maximum width of 800 at level of early gravid proglottides. Longest specimen with 222 proglottides. Proglottides craspedote, wider than long, except for a few final gravid ones that can be up to twice longer than wide. Scolex rounded, not markedly delineated from neck, 295-490 in diameter (367, n = 10) [312]. Suckers rounded, muscular, unarmed, 118-160 (142, n = 40) [135-145] in diameter. Rostellar sac regular, cylindrical, weakly muscular, extending well past level of posterior margin of suckers into anterior strobila, 342-457 x 123-175 (390 x 146, n = 10) [342 x 123]. Rostellum elongated, very muscular, with well developed glandular tissue, especially in it posterior half, 258-358 x 86-133 (323 x 112, n = 10) [290 x 186] (Fig. 1). Hooks on two rows, 24-26 [26] in number; similar in shape in both rows with long handles and blades, and well developed guards, that are forward oriented. Hooks of first row slightly shorter and straighter than those of second row. Hooks length 62-65.5 on first row (64, n = 13) and 66.5-69.5 on second row (68, n = 11) (Fig. 2). Neck poorly marked; proglottization distinct at 400-550 from posterior margin of suckers. Genital pores lateral, situated slightly anterior to mid-length of lateral proglottis margin, irregularly alternating in very short series, e.g. …, 3, 2, 3, 2, 2, 1, 2, 1, 2, 1, 1, 1, 2, 1…; or …, 2, 1, 1, 1, 1, 4, 2, 1, 1, 2, 1, 1, 1, 3, …, no more than 5 consecutive pores observed on a single side. Ventral osmoregulatory canals up to 55 wide, possibly more in terminal proglottides, connected posteriorly in each proglottis by transverse anastomosis. Dorsal osmoregulatory canals 5-12 wide. Genital ducts passing between osmoregulatory canals. Genital atrium small, unremarkable, sink-shaped, up to 20 deep and 30 in diameter.

Testes numerous, 24-34 (29.5, n = 40) [25-30] in number; in 2-3 layers, in one continuous, transversely elongated posterior field, may occasionally overlap posterior lobes of ovary or osmoregulatory canals (Fig. 3). External vas deferens convoluted antero-porally, behind proximal extremity of cirrus-sac. Cirrus-sac weakly muscular, straight and elongate, 96-140 x 30-45 (114 x 37, n = 44) [101-112 x 36-40]; most commonly not reaching osmoregulatory canals, or just overlapping them. Internal vas deferens forming several coils. Cirrus armed with typical terminal dense tuft of hair, reaching 20-31 (26, n = 28) in length. No evaginated cirrus observed. Ductus masculinus very short, often difficult to see or absent (Fig. 4).

Vitellarium central, compact with irregular large lobes, transversely elongated, variable in shape, most often forming a flattened V, and becoming straighter in older mature proglottides; reaching up to 325 x 65. Ovary, antero-central, transversely elongated, mostly compact with poorly marked lobules, reaching longitudinal osmoregulatory canals on both sides. Mehlis' gland subglobular, anterior to vitellarium. Seminal receptacle round, becoming more oval when full but never elongated; reaching up to 185 x 115 in late mature and pregravid proglottides; dorsal and between ovary wings, anterior to poral part of vitelline gland. Vagina opened posteriorly to male pore, very long, straight and transverse, parallel and ventral to cirrus-sac; thick-walled; not divided into copulatory and conductive part; surrounded by a loose irregular sheath; no vaginal sphincter (Fig. 3).

Uterus starts its development in late mature proglottides as a diffuse ventral reticulum, progressively forming numerous small lobes and occupying entire median field; crossing osmoregulatory canals and extending in lateral fields. Uterus eventually becoming sacciform with deep, progressively disappearing septa. Eggs oval with thick embryophores 41-54 x 35-48 (49 x 40, n = 22). Oncospheres 26-36 x 20-28 (30 x 24, n = 25). No polar processes. Central embryonic hooks slightly longer 16-18 (17, n = 14), and thinner than lateral ones 14-16 (15, n = 20). Lateral embryonic hooks similar within each pair (Fig. 5).

Remarks: This material has first been reported, albeit without discussion, in Mariaux (1994) under the name



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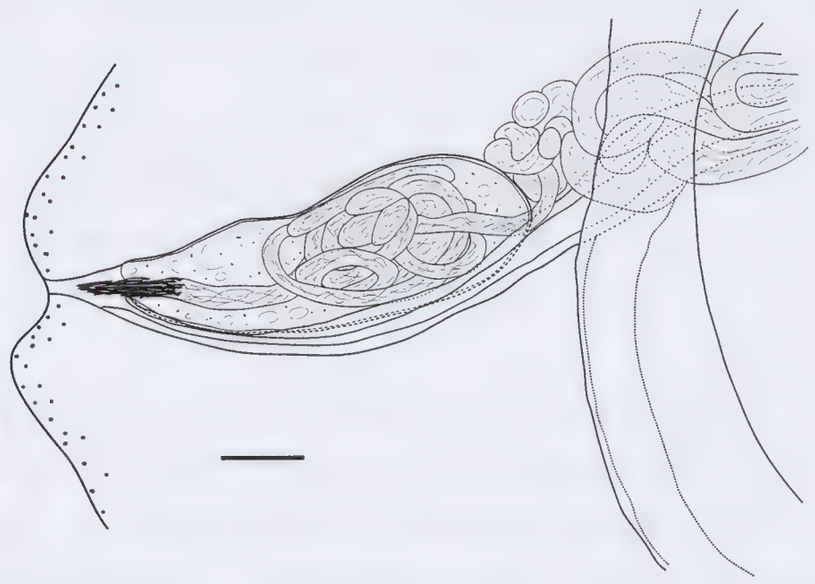

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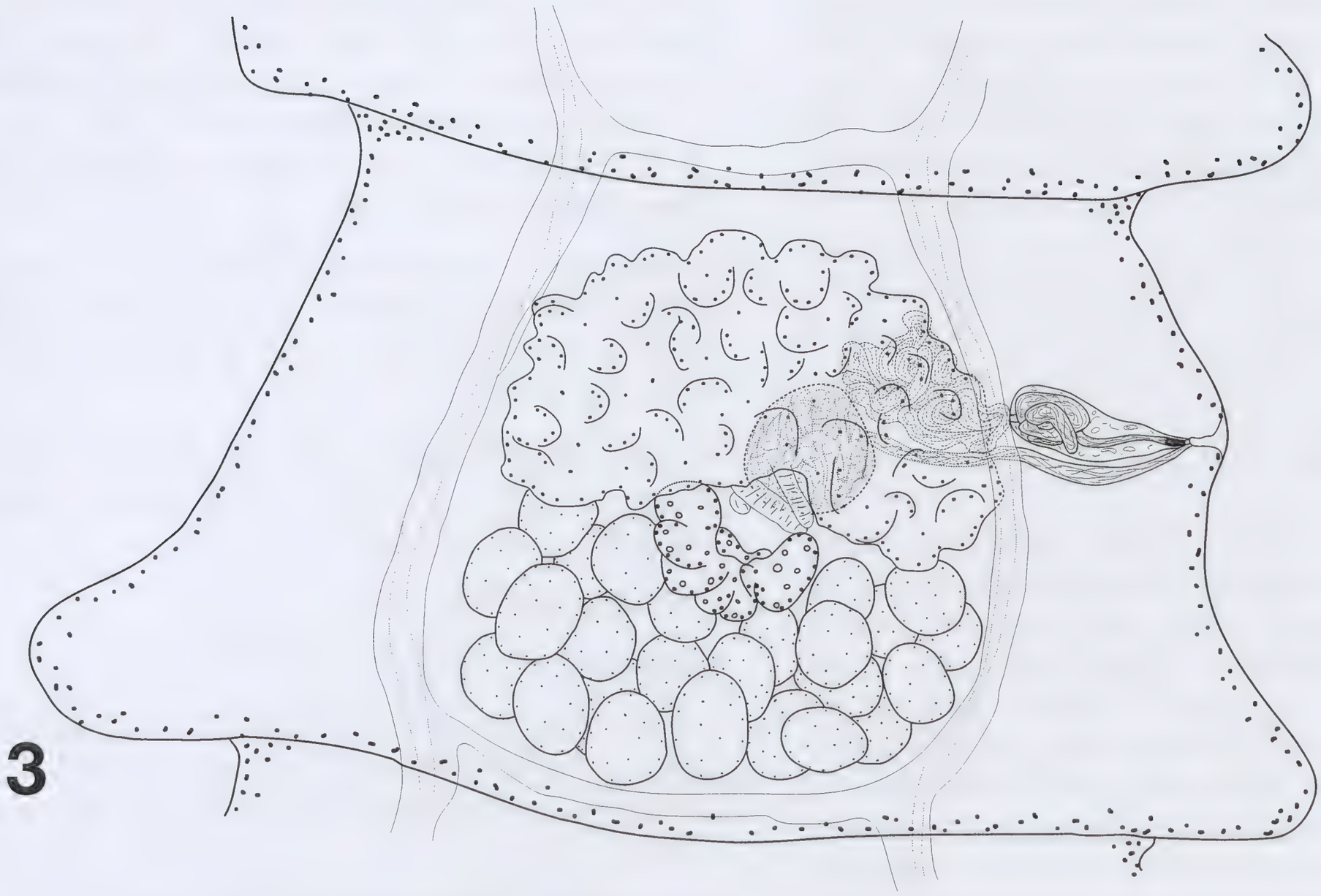

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Figs 1-5. *Spiniglans thomassankara* sp. nov. (1) Scolex. (2) Rotellar hooks. (3) Mature proglottis, ventral view; (4) Terminal genitalia. (5) Egg. Scale bars: 1, 3: 100 µm; 2: 50 µm; 4, 5: 20 µm.

Anomotaenia sp. Meanwhile Bona (1994) proposed a comprehensive synthesis of the Dilepididae systematics, which, essentially, is still accepted today (Mariaux *et al*., 2017).

In Bona (1994), the group of genera defined by the presence of tufts of bristle-like spines on the cirrus is well defined but its organization is particularly challenging. Generic diagnoses are complex and sometimes based on difficult to observe or non-classical characters. The present material shows affinities both with *Dictymetra* Clark, 1952 and *Spiniglans* Yamaguti, 1959. It resembles *Dictymetra* in having clearly defined rows of rostellar hooks with comparatively long blades; no, or very poorly marked, ovary isthmus; and rather long cirrus bristle. On the other hand the following characters make it closer to the definition of *Spiniglans*: proglottides generally wider than long; very long vagina; extremely short, often not visible ductus masculinus; testes in transverse field and, possibly, absence of polar process in the eggs (although the latter character is certainly variable in *Dictymetra*, especially for its terrestrial species).

Clearly, the generic placement of this material may consequently only be provisional until this whole group of species is reassessed. In the meantime, I favor a placement in *Spiniglans*, essentially because of the nearly complete absence of ductus masculinus. A comparison with members of both genera remains nevertheless obviously needed.

Dictymetra and *Spiniglans* have recently been reviewed and discussed by Mariaux & Georgiev (2018) who also provided a list of accepted species for both genera. They noted the heterogeneous host spectrum of *Dictymetra* and its possible paraphyly. Indeed, *Dictymetra* is mostly found in Charadriiformes worldwide, although a few species have also been recorded in terrestrial birds, including one in Passeriformes. The 13 known species in the genus show a global distribution, including in Africa. The present material differs from all species listed by Mariaux & Georgiev (2018, see their table 4) mostly by its rostellum size, length of hooks and number of testes. It is however similar to *D. belopolskajae* Spasskaya & Spasskii, 1973, a parasite of Alaudidae in Russian Arctic (Spasskaya & Spasskii, 1973), but can be distinguished from it by showing 24-26 rostellar hooks (vs. 20 in *D. belopolskajae*).

Members of *Spiniglans* are almost all found in Corvidae, from Europe to Australia, but the type species, *Spiniglans microsoma* (Southwell, 1922), was described from a ploceid (and an emberezid) in India (Southwell, 1922). All seven species recognized by Mariaux & Georgiev (2018, see their table 2) differ from the present material by their hooks number and length as well as by their testes number (our observations of *S. microsoma* type material revealed a slightly smaller scolex and suckers diameters than originally reported but no major discrepancies with the original description). In consequence, it belongs to a new species, *Spiniglans thomassankara* sp. nov. The genus' range is extended to Africa and consequently to the complete Old World.

Weavers are common sights throughout Africa and Ploceidae form a well-diversified family with over 100 recognized species. Their cestode fauna is nevertheless practically unknown, with *Anomotania quelea* (Mettrick, 1961) from *Quelea quelea* (Linnaeus, 1758) in Zambia being the only exception I am aware of. Although being quite similar to our material, the latter species differs from it by a smaller number of testes and a longer cirrus-sac that is lacking any armature (Mettrick, 1961).

S. thomassankara is locally relatively abundant in its type host (19% prevalence) but much less so in the other two congeneric hosts in which it was found. It has not been found neither in other sympatric *Ploceus* potential hosts [e. g. *P. aurantius* (Vieillot, 1808), 17 examined; *P. heuglini* Reichenow, 1886, 2 examined] nor in other common Ploceidae taxa in the same area (e. g. belonging to *Malimbus* or *Vidua*) or other parts of the country (e. g. belonging to *Euplectes* or *Plocepasser*). Lagunae from Southern Ivory Coast constitute a particular, and endangered, ecosystem belonging to the "Guinean mangroves ecoregion" that extend from Senegal to Ivory Coast (Burgess *et al*., 2004; Carr *et al*., 2015). Should *S. thomassankara* intermediate hosts be linked to this peculiar environment, the species may possibly be endemic to the region.

Monopylidium comoensis sp. nov.

Figs 6-9

Holotype: MHNG-PLAT-0016113 (formerly MHNG 987.276); Côte d'Ivoire, Zanzan, Ouango Fitini, Northern edge of Comoé National Park, surroundings of former airfield; WGS84 9.58, -4.01; 300 m; 22.01.1987. From *Gymnoris dentata* (Sundevall, 1850) (Passeriformes, Passeridae).

Paratype: MHNG-PLAT-0016112 (formerly MHNG 987.275); MHNG-PLAT-0137403 (formerly MHNG 987.276). Same data as holotype. MHNG-OIS-1773.015.

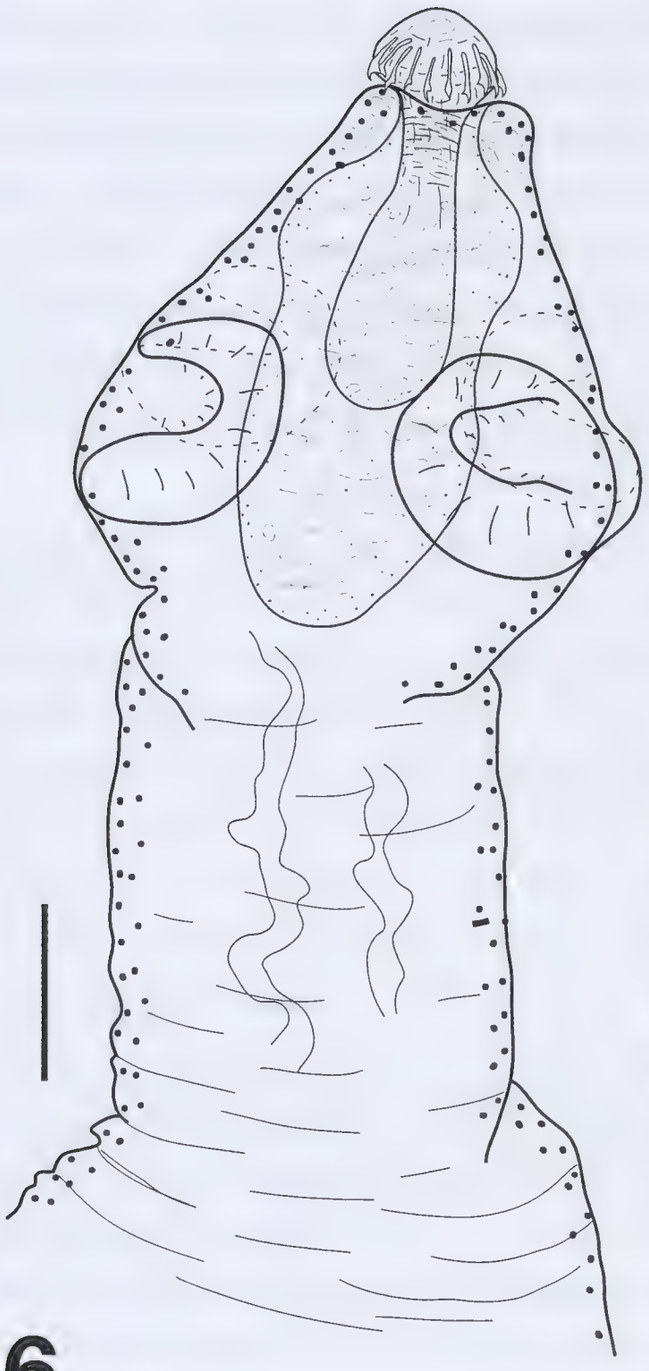
Comparison material studied: MHNG-PLAT-0044433, 1 slide. *Monopylidium barbara* (Meggitt, 1926), "cotype".

Prevalences: 2/17 (12%).

Intensity: 2.

Etymology: The species is named after the National Park of the Comoé, and the eponym river flowing through it, in the North Eastern corner of the Côte d'Ivoire.

Description: Worm with body of medium size, up to 33 mm in length and with maximum width of 1000 at level of early gravid proglottides. Longest specimen



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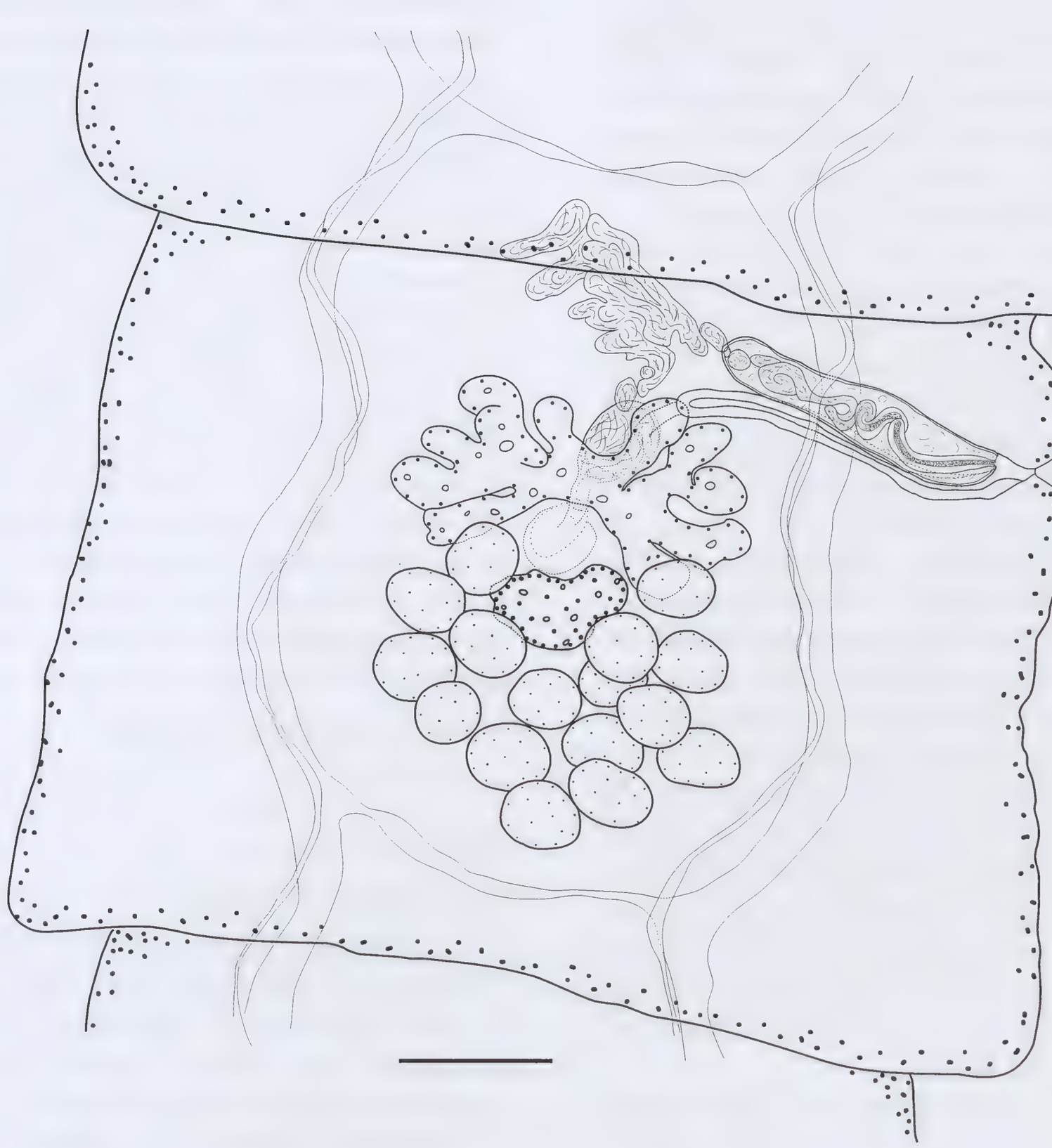

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Figs 6-9. *Monopylidium comoensis* sp. nov. (6) Scolex. (7) Rostellar hook. (8) Mature proglottis, dorsal view (9) Terminal genitalia. Scale bars: 6, 9: 50 µm; 7: 10 µm; 8: 100 µm.

with 139 proglottides, but fully gravid specimens must be longer. Proglottides craspedote, wider than long, progressively becoming square then longer than wide when pregravid (up to 1.6x longer than wide in our material). Scolex elongated, quite narrow and pointed, well delineated from neck, 138 in diameter (n = 2). Suckers small, rounded, muscular, unarmed, 60-68 (64, n = 8) [62-68] in diameter. Rostellar sac very large, cylindrical, very glandular, extending past level of posterior margin of suckers, 162 x 68 (n = 1). Rostellum elongated, with well-developed glandular tissue, 105 x 30 (n = 1) (Fig. 6). Hooks very short, on two poorly demarcated rows, 20-22 in number [20]; similar in shape in both rows, with short blades, strong handles and long, very slightly curved handles. Hooks from first row marginally shorter than those from second row. Hooks length 13.5-15.5 on first row (14.5, n = 9) and 14.5-16.5 on second row (15.5, n = 9) (Fig. 7). Neck well-marked; proglottization distinct at about 220-270 from posterior margin of suckers. Genital pores lateral, opening at about 25-30% of lateral proglottis margin length, irregularly alternating in very short series, with some zones of regular alternations. e.g. …, 2, 1, 1, 4, 1, 1, 1, 1, 1, 1, 1, 1, 1, 2, 4, 2, 1, …; no more than 5 consecutive pores observed on a single side. Ventral osmoregulatory canals generally 25-35 (but up to 50) wide, connected posteriorly in each proglottis by transverse anastomosis. Dorsal osmoregulatory canals narrow 3-5 wide. Genital ducts passing between osmoregulatory canals. Genital atrium small, sink-shaped, up to about 25 deep and 30-40 in diameter.

Testes numerous, 14-25 (19, n = 34) [16-22] in number; in a single layer, in one continuous, posterior field, extending anteriorly to posterior level of ovary (Fig. 8). External vas deferens convoluted antero-porally. Cirrus-sac weakly muscular, straight, long, 172-212 x 38-60 (195 x 44, n = 22); always crossing osmoregulatory canals. Internal vas deferens forming several coils. Cirrus armed, lined with very small spines (Fig. 9).

Vitellarium central, compact, subglobular, usually somewhat transversely elongated, but variable in shape; 85-125 x 55-95 (102 x 73, n = 12). Ovary, antero-central, clearly bi-winged and multilobulated, with about 5-6 deep main lobules on each side. Mehlis' gland globular, anterior to vitellarium, in between ovary wings. Seminal receptacle elongated to oval; discrete; reaching up to 112 x 73; dorsal and slightly anterior to ovary wings. Vagina opened posteriorly to male pore, straight and transverse, long, possibly reaching up to seminal vesicle, parallel and ventral to cirrus-sac; particularly thick walled, surrounded by a compact sheath of large cells; its poral opening often enlarging in a well marked V-shaped, funnel like structure (Figs 8, 9).

Eggs appearing progressively, alone or in small groups in the whole parenchyma, with uterus border not clearly visible. Uterus becoming densely reticulate/multilocular, but its final stage of development, as well as fully developed eggs not available in our material.

Remarks: This material belongs to the genus *Monopylidium* Fuhrmann, 1899 as defined by Spasskii (1993) and accepted by Mariaux & Georgiev (2018). A list of species in this genus, together with a summary of their main characters was provided by Mariaux & Georgiev (2018, see their table 3), and most of them can easily be distinguished from the present material on the basis of their different rostellar hooks size and number; testes number or cirrus sac dimensions.

Two species are however similar to our specimens: *M. passerinum* Fuhrmann, 1907 was found in Passeriformes, including various Passeridae (Matevosyan, 1963) and has a large distribution (Palaearctic, Australia). It was initially described by Fuhrmann (1907) and a detailed description was provided by Johnston (1909). Despite their close resemblance, especially in rostellar structures, our material definitely differs from *M. passerinum* by a lower number of testes (14-25 vs 25-30), and accessorily, by slightly smaller suckers and larger vitelline glands. Additionally, *M. barbara* (Meggit, 1926) and *M. innominata* (Meggit, 1926), both from Yangon, Myanmar (ex Rangoon, Burma) were also described from Passeridae (Meggitt, 1926), the latter taxon being subsequently synonymized with the former (Southwell, 1930). *Monopylidium barbara* is only succinctly described but essentially differs from the new species in having 23 rostellar hooks. A small fragment of this species cotype, from *Passer montanus* (Linnaeus, 1758) in Rangoon, was also examined. Only a few male proglottides allow for meaningful observations and they show a shorter cirrus sac (133-150) and a higher number of testes (24-31) than in the original description. Although limited, these observations also allow differentiating *M. barbara* from the present material.

The Sahel bush sparrow, or bush petronia, *Gymnoris dentata*, is presently placed within the family Passeridae, but was previously considered a Ploceidae (in the genus *Petronia*). *Monopylidium comoensis* has not been found in any other member of these families during our surveys. In the same locality, bush petronias are also hosts of a *Biuterina* species that we described previously (Georgiev & Mariaux, 2007), but are not known to harbor any other cestode throughout their range.

DISCUSSION

Our findings highlight the considerable potential for discovering unknown parasite taxa, in the most common and widespread hosts. This should encourage a more systematical exploration of this fauna. As evidenced here, and at multiple occasions, abundant and unremarkable, but understudied, bird species host a significant diversity of parasites [e.g., specifically for cestodes: Mariaux (1994) in Ivory Coast; Gigon & Beuret (1991) in Switzerland or Mariaux & Georgiev (2018) in Australia]. Unfortunately, due to excessively

rigid protection schemes, taxonomists are now mostly prevented to access this component of biodiversity, making the exploration and description of this fauna practically impossible in many parts of the world. This is an unfortunate consequence of, obviously well intended legal or administrative decisions, eventually becoming counterproductive in some of their fields of application, such as our quest for global taxonomic knowledge.

ACKNOWLEDGEMENTS

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REFERENCES

Bona F.V. 1994. Family Dilepididae Railliet & Henry, 1909 (pp. 443-554). *In*: Khalil L.F., Jones A., Bray R.A. (eds), Keys to the cestode parasites of vertebrates. *CAB International, Wallingford*, 751 pp.

Burgess N.D., Hales J., Underwood E., Dinerstein E., Olson D., Itoua A., Schipper J., Ricketts T., Newman K. 2004. Terrestrial ecoregions of Africa and Madagascar: A conservation assessment. *Island Press, Washington DC, USA*, 544 pp.

Carr J., Adeleke A.W., Angu Angu K., Belle E., Burgess N., Carrizo S., Choimes A., Coulthard N., Darwall W., Foden W., Garreau J.-M. Gatarbirwa W., Hicks C., Kapijimpanga D.R., King E., Koenig K., Martinez S., Meng H., Kyame S.K., Polidoro B., Regnaut S., Shenann-Farpon Y., Shepherd G., Smith K., van Soesbergen A., Somda J., Walters G. 2015. Ecosystem profile Guinean Forests of West Africa biodiversity hotspot. *Critical Ecosystem Partnership Fund (CEPF) Report, Washington DC, USA,* 384 pp.

Clark D.T. 1952. Three New Dilepidid Cestodes, *Dictymetra numenii* n. gen. n. sp.; *Dictymetra paranumenii* n. sp. and *Anomotaenia filovata* n. sp. *Proceedings of the Helminthological Society of Washington* 19: 18-27.

Fuhrmann O. 1899. Mitteilung über Vogeltänien. III. *Taenia musculosa* Fuhrm. und *T. crateriformis* Goeze (*Monopylidium* nov. gen.). *Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten I. Abt. Originale* 26: 622-627.

Fuhrmann O. 1907. Bekannte und neue Arten und Genera von Vogeltänien. *Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten I. Abt. Originale* 45: 516-536.

Georgiev B.B., Mariaux J. 2007. Cestodes of the genus *Biuterina* Fuhrmann, 1902 (Cyclophyllidea: Paruterinidae) from passeriform and piciform birds in the Ivory Coast, with a key to the species of the genus. *Revue suisse de Zoologie* 114(1): 141-174. DOI: 10.5962/bhl.part.80392

Gigon P., Beuret J. 1991. Contribution à la connaissance des helminthes d'oiseaux dans le nord-ouest de la Suisse. *Revue suisse de Zoologie* 98(2): 279-302. DOI: 10.5962/bhl.part.79792

Johnston T.H. 1909. On the anatomy of *Monopylidium passerinum* Fuhrmann. *Journal and Proceedings of the Royal Society of N. S. Wales* 43: 405-411.

Lepage D. 2021. Avibase – the world bird database. Available from http://avibase.bsc-eoc.org [accessed 20 Apr. 2021]

Mariaux J. 1994. Avian cestodes of the Ivory Coast. *Journal of the Helminthological Society of Washington* 61(1): 50-56. http://bionames.org/bionames-archive/issn/1049-233X/61/50.pdf

Mariaux J., Georgiev B.B. 2018. Seven new species of cestode parasites (Neodermata, Platyhelminthes) from Australian birds. *European Journal of Taxonomy* 440: 1-42. DOI: 10.5852/ejt.2018.440

Mariaux J., Georgiev B.B. 2020. Cestode parasites (Neodermata, Platyhelminthes) from Malaysian birds, with description of five new species. *European Journal of Taxonomy* 616: 1-35. DOI: 10.5852/ejt.2020.616

Mariaux J., Tkach V.V., Vasileva G.P., Waeschenbach A., Beveridge I., Dimitrova Y.D., Haukisalmi V., Greiman S.E., Littlewood D.TJ., Makarikov A.A., Philips A.J., Razafiarisolo T., Widmer V., Georgiev B.B. 2017. Cyclophyllidea van Beneden in Braun, 1900. *University of Kansas, Natural History Museum, Special Publication* 25: 77-148. https://core.ac.uk/download/pdf/323992051.pdf

Matevosyan E.M. 1963. Dilepidoidea – Tapeworms of Domestic and Wild Animals. Osnovy Tsestodologii. *Izdatel'stvo Akademii Nauk SSSR, Moscow*, 687 pp.

Meggitt F.J. 1926. On a Collection of Burmese Cestodes. *Parasitology* 18 (2): 230-237. DOI: 10.1017/S0031182000005199

Mettrick D.F. 1961. A new cestode *Anomotaenia quelea* sp. nov. from the red-billed quelea, *Quelea quelea* (L.). *Journal of Natural History* 4 (46): 589-592. DOI: 10.1080/00222936108651184

Southwell T. 1922. Cestodes from Indian birds with a note on *Ligula intestinalis*. *Annals of Tropical Medicine and Parasitology* 16(4): 355-382. DOI: 10.1080/00034983.1922.11684330

Southwell T. 1930. Cestoda Volume 2. The Fauna of British India, Including Ceylon and Burma. *Taylor & Francis, London*, 262 pp. http://cslrepository.nvli.in//handle/123456789/8343

Spasskaya L.P., Spasskii A.A. 1973. *Dictymetra belopolskaje*, sp. n. (Cestoda: Dilepididae) a new species of cestode in birds. *Izvestiya Akademii Nauk Moldovskoi SSR (Biologicheskie i Khimicheskie Nauki)* 4: 63-68.

Spasskii A.A. 1993. On the structure of species of genus *Monopylidium* (Dilepididae) and its position in Sestoda [Cestoda] system. *Buletinul Academiei de Stiinte a Republicii Moldova Stiinte Biologice si Chimice* 1: 42-49.

Yamaguti S. 1959. Systema helminthum. Vol. II. The cestodes of vertebrates. *Interscience Publishers, New York*, 860 pp.

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New genera and species of Afrotropical Ancylolomiini Ragonot, 1889 (Lepidoptera: Pyralidae *sensu lato*: Crambinae)

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Abstract: Two new genera of Afrotropical Crambinae are described and illustrated: *Afrocharltona* gen. n. including *A. katanga* sp. n. from the Democratic Republic of the Congo and *A. oblongissima* sp. n. from Botswana, Namibia and Zambia, and *Afroromieuxia* gen. n. including *A. aarviki* sp. n. from Tanzania, *A. bernardlandryi* sp. n. from the Democratic Republic of the Congo, and *A. ustjuzhanini* sp. n. from Zambia.

Keywords: Africa - *Afrocharltona* - *Afroromieuxia* - Crambidae - Pyraloidea.

INTRODUCTION

The tribe Ancylolomiini Ragonot, 1889 experienced important evolutionary success in the Old World and particularly in the Afrotropics. Recent genetic studies (Léger *et al*., 2019) highlight that the Ancylolomiini should enclose the Prionapterygini Landry, 1995, but for the sake of simplicity the present paper concerns only the genera strictly related to *Ancylolomia* Hübner, 1825, as summarized in Bassi (2013). The Afrotropical fauna of the tribe's main genera, i.e. *Ancylolomia*, *Prionotalis* Hampson, 1919, *Charltona* Swinhoe, 1886, were never reviewed, except for two small species groups of *Ancylolomia* (Bassi, 2013).

Among the very valuable material forwarded to me for study by Leif Aarvik (Natural History Museum, University of Oslo, Norway) and by Bernard Landry (Muséum d'histoire naturelle, Geneva, Switzerland), and in my own collection I found a few species that are superficially similar to known genera such as *Charltona*, *Diploschistis* Meyrick, 1937 and *Prionotalis*, but that have such unique genitalia that the description of new genera is deemed to be warranted.

MATERIAL AND METHODS

Genitalia preparations were made following Robinson (1976). The terminology of the genitalia follows Błeszyński (1970), Klots (1970) and Kristensen (2003). Genitalia photographs were taken with a Canon S120 digital camera. The habitus photos were made with a Nikon D300 digital camera. The images were enhanced with Adobe Photoshop Elements. The following abbreviations are used: 'BC' for barcode, 'DRC' for Democratic Republic of the Congo', 'GB' for Graziano Bassi, 'GS' for genitalia slide', 'm' for meter(s), 'RCGB' for Graziano Bassi research Collection, Avigliana, Italy, 'MHNG' for "Muséum d'histoire naturelle de Genève," Geneva, Switzerland, 'NHMO' for Natural History Museum, University of Oslo, Norway, 'RMCA' for Royal Museum for Central Africa, Tervuren, Belgium, 'ZSM' for Zoologische Staatsammlung München, Germany, 'TMSA' for Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria, Republic of South Africa.

TAXONOMY

Afrocharltona gen. n.

Figs 7-11, 13, 17-19

Type species: *Afrocharltona oblongissima* sp. n.

Diagnosis: In the adult the slender forewing distinguishes *Afrocharltona* from *Charltona*. Some *Prionotalis* [i.e. *P. balia* (Tams, 1932)] also have forewing yellow marbled with brown, but their apex of forewing is more pointed. In the male genitalia the combination of modified uncus and the very long and narrow valva represents a distinctive feature. In the female genitalia the lateral extension of medium length branching off in the middle of the ductus bursae and the ductus seminalis originating close to the lateral

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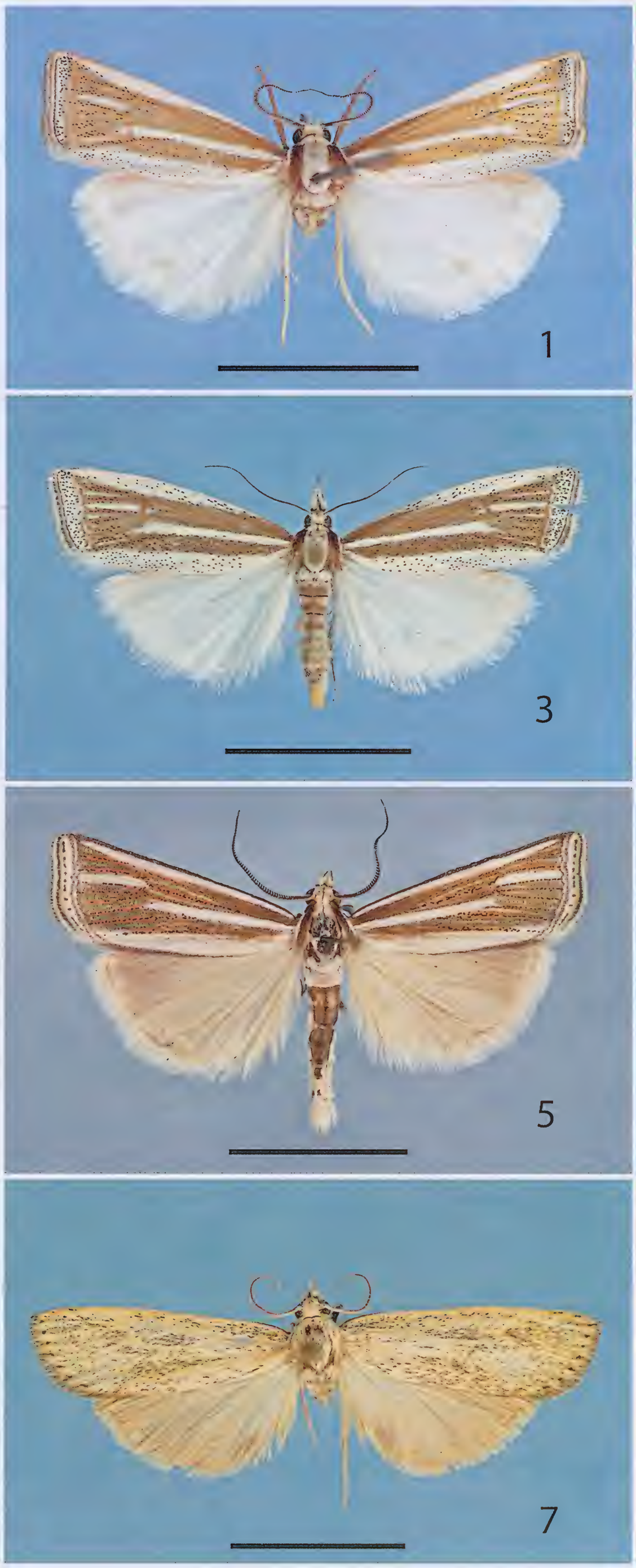

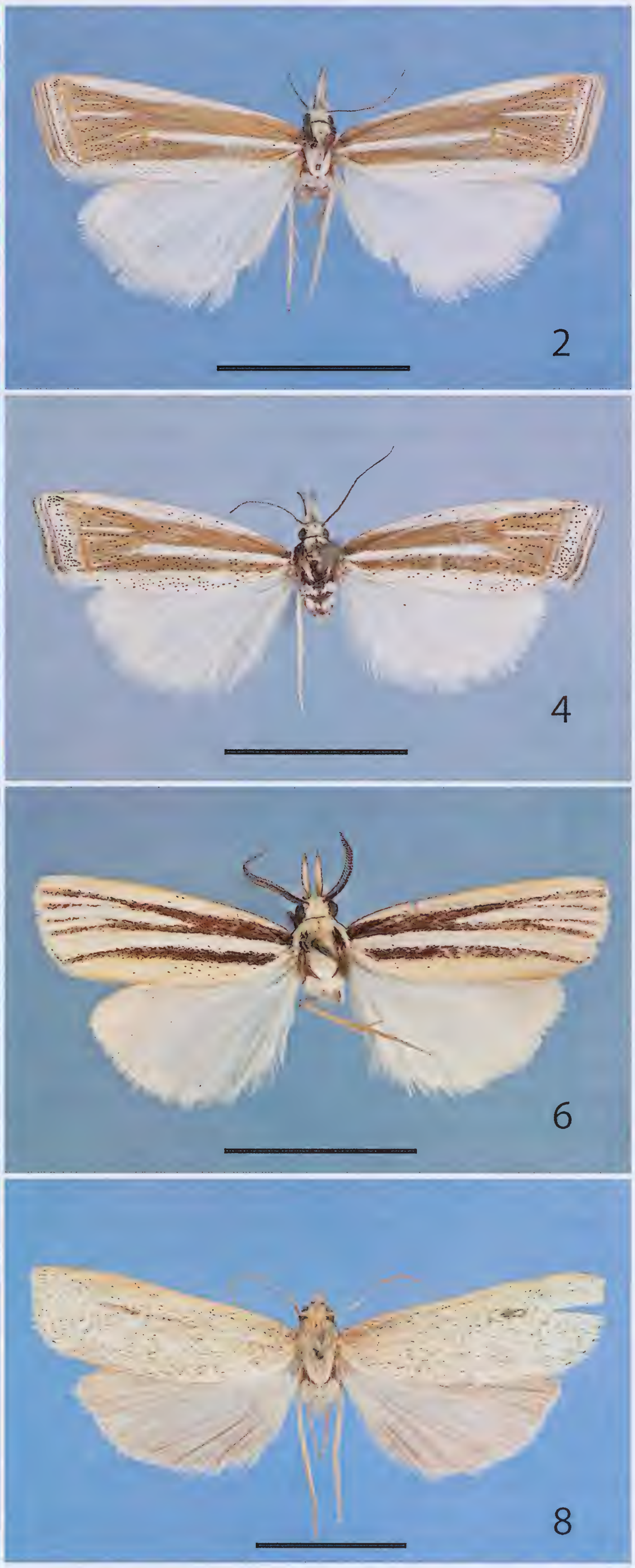

Figs 1-8. Habiti. (1) *Afroromieuxia bernardlandryi*, holotype. (2) *A. bernardlandryi*, female paratype. (3) *A. aarviki*, holotype. (4) *A. ustjuzhanini*, holotype. (5) *Ancylolomia prepiella*, male, Lesotho. (6) *Diploschistis stygiocrena*, male, DRC. (7) *Afrocharltona oblongissima*, holotype. (8) *A. katanga*, holotype. Scale bars = 10 mm.

extension, are unique among related genera except for the *prepiella* species complex in the *inornata* group in *Ancylolomia* (Bassi & Trematerra, 2014). In this complex, however, the lateral extension is always very thin.

The holotype and the female paratype from Zambia of *A. oblongissima* are barcoded, showing intraspecific distance of 1.27% and distance of 9.36% from *Charltona tritonella* (Hampson, 1898) and 7.74% from *Charltona plurivittalis* Hampson, 1910. However, the paucity of available barcoded specimens of *Ancylolomia* and allied genera does not allow a comprehensive DNA comparison, and in the future more molecular markers should be analysed to be conclusive on the relationships to other genera of Ancylolomiini.

Etymology: The generic name is a combination of *afro* (from Africa) and *Charltona*, the probably closest genus. The gender of the new genus is feminine.

Description: Medium to large species, with labial palpi rather short (2.5 - 3 x eye diameter in side view), ocelli and chaetosemata poorly developed, narrow forewing with rounded apex and arched termen.

Male genitalia. Uncus slightly longer than gnathos (1.1 x), heavily bulged dorsally and with blunt and wrinkled apex. Gnathos subtriangular, slightly upcurved apically. Tegumen with slender arms, tegumen roof 0.3 of tegumen arm length. Vinculum v-shaped, moderately produced dorsally. Juxta suboval, more or less folded medially. Pseudosaccus a small plate fused with juxta. Valva strongly elongated, tapering towards apex; costal process always developed over cucullus. Phallus stout, 0.6 x valva length, with phallobase downcurved.

Female genitalia. Papillae anales subtriangular, rounded ventrally. Apophyses well developed, roughly the length of papillae anales. Ostium concave, with sclerotized edge. Ductus bursae elongated, sclerotized and bearing a narrow lateral extension. Ductus seminalis originating at the middle of ductus bursae. Corpus bursae oval, wrinkled.

Biology: Unknown.

Distribution: Central Africa and Northern part of Southern Africa.

Afrocharltona oblongissima sp. n.

Figs 7, 9-11, 17-19

Material examined

Holotype: Male; Botswana, Maun, 957 m, 1-2.xii.2010, 19°55'58S 23°30'61E, lux, G. Bassi legit, BC 92320 ZSM, GS 6245 GB, 41400 RCGB.

Paratypes: Male; same data as holotype, Collezione Bassi, GS 5365 GB, RCGB. – Female; Zambia, Livingstone, Maramba River Lodge camp, 17°53'S 25°51'E, 900 m, 28.xi.2010, lux, G. Bassi legit, BC 92321 ZSM, GS 6230 GB, RCGB. – Female; Namibia, Ghaub Vall[ey], 7.i.[19]72, D. M. Kroon [legit], GS 5444 GB, TMSA. – Female; Namibia, Otavi, 5.i.[19]72, D.M. Kroon [legit], TMSA.

Diagnosis: The yellow ground colour distinguishes *A. oblongissima* from *A. katanga* described below. The male genitalia are similar to *A. katanga* but the valva and apical thorn of the costal arm are longer and the phallus is without cornuti in the vesica. The female genitalia with lateral extension of medium length and thickness, with ductus seminalis originating nearby from ductus bursae are unlike every other species of the *Ancylolomia* complex.

COI barcode sequence of the holotype BIN: BOLD:ADF2943 (658 bp):

AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATATT-
AGGAACATCTTTAAGACTTTTAATTCGAGCTGAATTAG-
GAAATCCTGGATCTTTAATTGGAGATGATCAAATTTATAATAC-
TATTGTAACAGCTCATGCATTTATTATAATTTTTTTTATAGT-
TATACCAATTATAATTGGTGGATTTGGTAATTGATTAGTC-
CCTTTAATATTAGGAGCACCTGATATAGCTTTCCCCCG-
TATAAATAATATAAGATTTTGATTACTACCTCCCTCTCTA-
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CAGGTACTGGATGAACAGTGTACCCCCCACTTTCATC-
CAATATTGCTCATGGTGGAAGTTCTGTAGACCTAGC-
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TCTTTATCAACACTTATT

Etymology: The name is derived from the Latin *oblungus-a* = very elongated, and refers to the shape of the valva in the male genitalia.

Description (Fig. 7): Wingspan of holotype 29 mm; male paratype 34 mm, female paratypes 33 to 36 mm. Labial palpus 3 x as long as greatest diameter of eye, ochre brown tipped with white on outer side, creamy white on inner side. Maxillary palpus ochre brown tipped with white. Frons rounded, slightly produced, white to pale yellow. Antennae thin, serrate in male, simple in female, pale brown with silvery white costa. Vertex white. Patagia white to pale yellow. Tegulae and thorax pale yellow sprinkled with brown. Forewing slender, with rounded apex and termen oblique; ground colour pale grey yellow sprinkled with brown and black; veins marked with yellow; seven terminal dots; fringes white and silvery grey; underside grey yellow strongly suffused with dark brown. Hindwing pale golden yellow suffused greyish brown; terminal line brown; fringes paler than ground colour; underside pale golden yellow suffused with brown. Legs golden yellow; tibial spurs small. Abdomen golden yellow suffused with grey, paler in males; sternites pale yellow.

Male genitalia. (Figs 10, 11). Uncus as long as gnathos, strongly bulged dorsally, with apex blunt and notched. Gnathos with pointed and slightly upcurved apex. Tegumen almost twice as long as uncus, narrow. Vinculum

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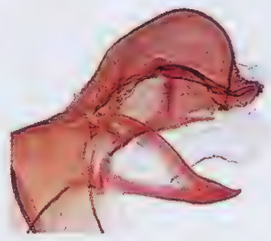

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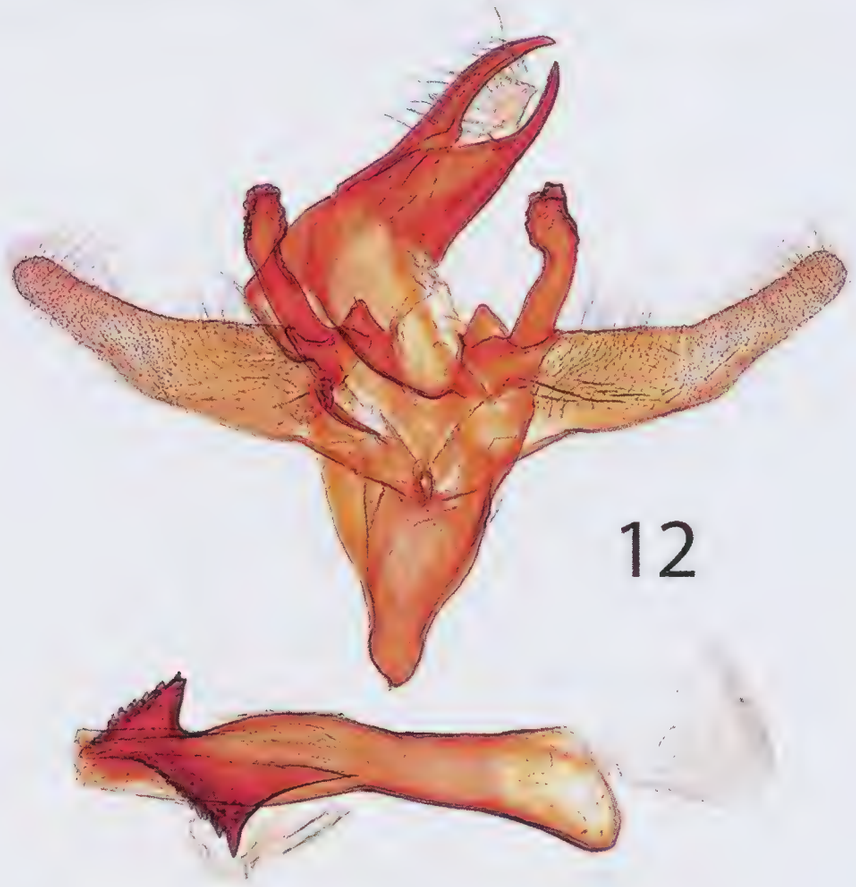

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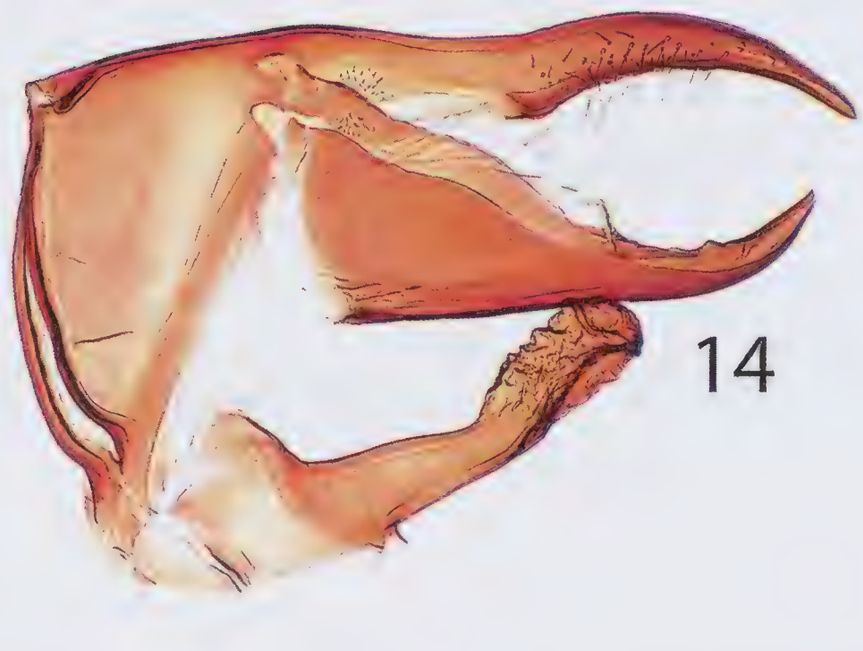

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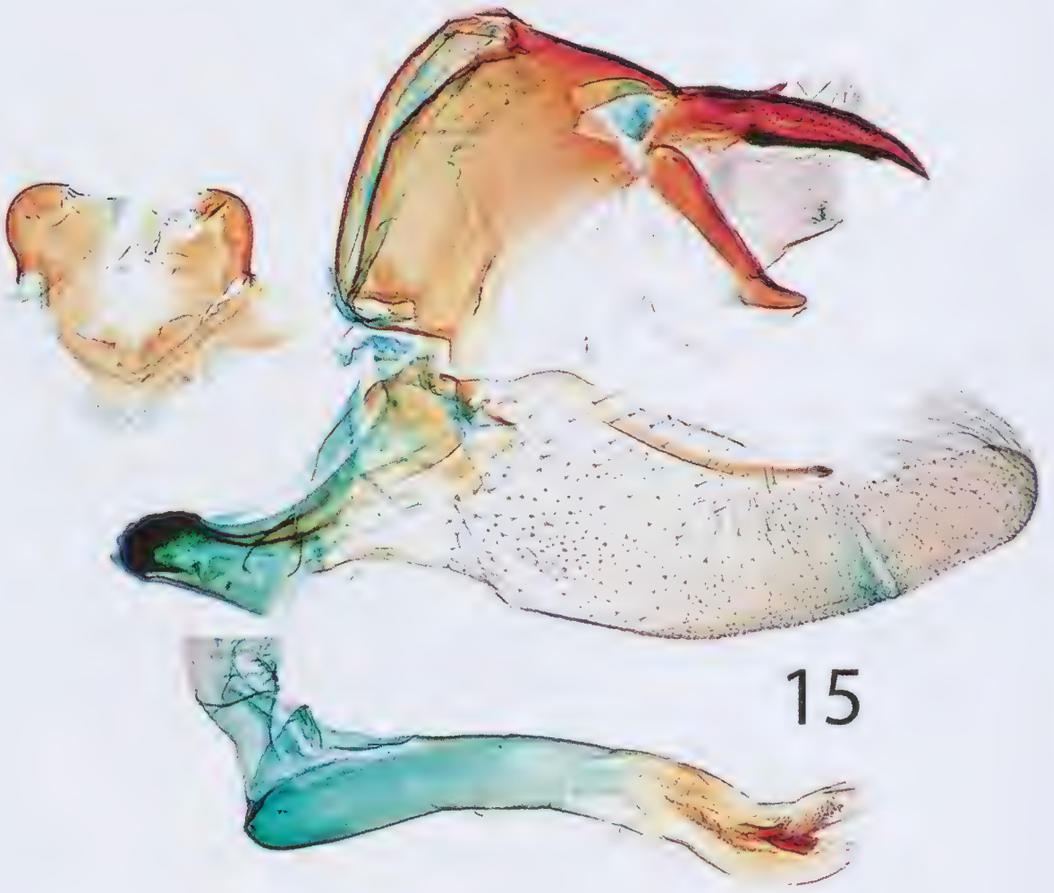

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Figs 9-15. Habitat and male genitalia. (9) Habitat of *Afrocharltona oblongissima* (photo G. Bassi, Dec., 2010). (10) *A. oblongissima*, holotype. (11) *A. oblongissima*, paratype, Botswana, Maun, uncus and gnathos in lateral view. (12) *Afroromieuxia bernardlandryi*, holotype. (13) *Afrocharltona katanga*, holotype. (14) *Afroromieuxia bernardlandryi*, paratype, uncus, gnathos and costal process in lateral view. (15) *Diploschistis stygiocrena*, DRC.

stout, subtriangular. Pseudosaccus subtrapezoidal, fused with juxta. Juxta broadly v-shaped. Valva extremely elongated, with rounded cucullus; costal arm slightly longer than valva, strongly sclerotized, with apical long and pointed thorn. Phallus with bent phallobase: vesica with minute scobinations.

Female genitalia (Figs 17-19). Papillae anales subtriangular. Apophyses posteriores with lightly sclerotized basis and arms weakly arched. Abdominal segment VIII ventrally membranous and lightly sclerotized dorsally. Apophyses anteriores sub-triangular, shorter than apophyses posteriores. Ostium bursae large, semicircular, lightly sclerotized. Ductus bursae twice as long as corpus bursae, sub-conical, strongly sclerotized except at its beginning; extension at 0.5, just below origin of ductus seminalis, cylindrical, slightly shorter than corpus bursae, more or less sclerotized and wrinkled. Corpus bursae sub-oval, weakly wrinkled.

Biology: Unknown. The adults from Botswana and Zambia were attracted to actinic artificial light in the riparian vegetation (Fig. 9).

Distribution: Northern part of Southern Africa: Botswana, Namibia, South Zambia.

Afrocharltona katanga sp. n.

Figs 8, 13

Material examined

Holotype: Male;[DRC], H[au]t Katanga, Tshinkolobwe, 5.x.[19]30, J. Romieux [legit], GS 5970 GB, MHNG.

Etymology: The species is named after the Province of the Democratic Republic of the Congo where the holotype was collected and is treated as a noun in apposition.

Diagnosis: The forewing with pale yellow ground colour flushed with pink grey and the brown hindwing with yellow, pink and grey suffusion distinguish *A. katanga* from *A. oblongissima*. The male genitalia are similar to those of *A. oblongissima* but the valva and apex of the costal arm are shorter and the phallus has two cornuti in the vesica.

Description (Fig. 8): Wingspan 36 mm. Labial palpus 2.5 x eye diameter, chestnut brown, apically paler. Maxillary palpus basally chestnut brown, apically paler. Antenna thickened, brown with costa paler. Frons rounded, slightly produced, off-white. Vertex and patagia pale yellow. Tegulae and thorax pale yellow, sprinkled with brown. Forewing and hindwing as in Fig. 8. Forewing sprinkled with brown, more intensely basally; suboval brown dot after cell; fringes bright ivory yellow. Underside pale yellow, suffused with brown dorsally in hindwing. Abdomen pale yellow. Legs yellow; tibial spurs asymmetrical, first pair longer than apical pair.

Male genitalia. (Fig. 13). Uncus as long as gnathos, strongly bulged dorsally and with apex blunt and notched. Gnathos with pointed and slightly upcurved apex. Tegumen almost twice as long as uncus, narrow. Vinculum stout, subtriangular. Pseudosaccus narrow, concave. Juxta suboval, with subtriangular protrusions medioventrally. Valva extremely elongated, narrowing apically, with rounded cucullus; costal arm slightly longer than valva, strongly sclerotized, with apical pointed thorn. Phallus with bent phallobase: vesica with two light sclerotized cornuti and minute scobinations. Female unknown.

Biology: Unknown.

Distribution: Presently known only from the Haut-Katanga province in the DRC.

Afroromieuxia gen. n.

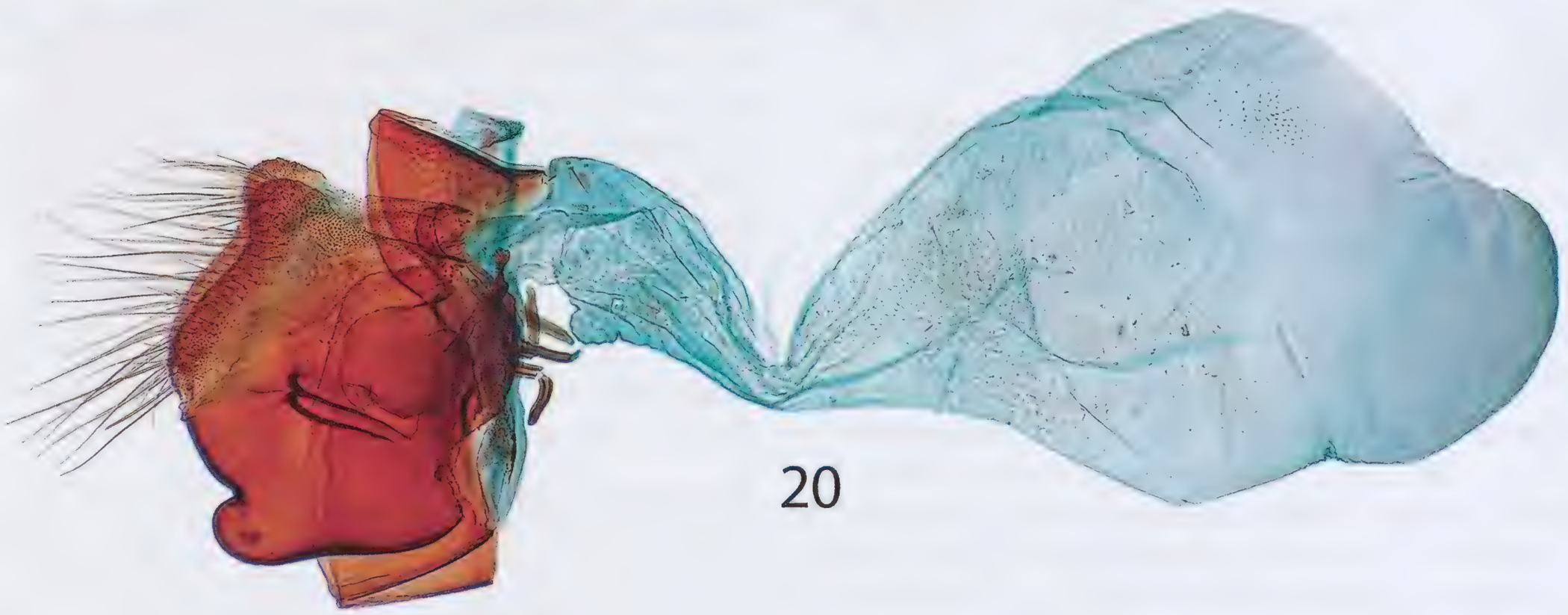
Figs 1-4, 12, 14, 16, 20, 22, 23

Type species: *Afroromieuxia bernardlandryi* sp. n.

Diagnosis: Adult features closely similar to some *Ancylolomia* [i.e. *A. prepiella* Hampson, 1919 (Fig. 5)], but in the latter the subterminal area is always sinuate with large black or dark brown dots. In the male genitalia the combination of strongly developed uncus and gnathos with the short and triangular tegumen and the strong pars basalis of the valva differ from related genera. In the female genitalia the heavily sclerotized ninth abdominal segment with the apophyses posteriores fused inside it, and the eighth abdominal segment – except for their apex –, are unique among Afrotropical Crambinae. *Diploschistis* with its sole species *D. stygiocrena* Meyrick, 1937, seems related to *Afroromieuxia* in the female genitalia (Fig. 21) with the ninth abdominal segment partially sclerotized, but its apophyses posteriores are not fused in the eighth abdominal segment and both adult (Fig. 6) and male genitalia (Fig. 15) are far from *Afroromieuxia* species.
DNA analysis of the holotype of *A. ustjuzhanini*, the more recent specimen studied, failed to provide any product usable for sequencing. Only future analysis could fully clarify the relationship with other genera of Ancylolomiini.

Etymology: The generic name is a combination of *afro* (from Africa) and Romieux, in honour of Jean Romieux (1893-1951) of Geneva, a pioneer of Lepidoptera research in the Democratic Republic of the Congo whose material was essential for the present study. The gender of the new genus is feminine.

Description: Medium to large species, with labial palpi long (3.5-4 x eye diameter in side view). Ocelli and chaetosemata well developed, subrectangular forewing, straight termen and well developed and straight subterminal fascia.



Figs 16-20. Habitat and female genitalia. (16) Habitat of *Afroromieuxia ustjuzhanini* (photo V. Anikin, Jan., 2011). (17) *Afrocharltona oblongissima*, paratype, Namibia. (18) *A. oblongissima*, paratype, Zambia. (19), ductus bursae with lateral extension. (20) *Afroromieuxia ustjuzhanini*, holotype.

Male genitalia. Uncus and gnathos fully developed. Tegumen subtriangular, with short arms; tegumen roof 0.5 x tegumen arm length. Vinculum stout, with arms subrectangular and strong dorsal projection. Juxta broad, v-shaped. Valva elongated, tapering towards apex; costal process strongly developed, 0.4 x valva length. Phallus stout, 1.3 x valva length, with two subapical lateral teeth. Female genitalia. Papillae anales well developed, concave. Apophyses posteriores fused inside eighth abdominal segment, with apex short. Sterigma rounded, slightly produced anteriorly. Ostium membranous. Ductus bursae 0.5 to 0.7 the length of corpus bursae, funnel-shaped. Ductus seminalis originating from posterior half of ductus bursae. Corpus bursae oval, without signa, but often with rows of spines.

Biology: Unknown.

Distribution: Central Africa, south to Northern Zambia.

Afroromieuxia aarviki sp. n.

Figs 3, 23

Material examined

Holotype: Female; Tanzania, Mufindi Distr[ict], Mufindi, 1960 m, 16.i.1993, leg[it] Leif Aarvik, GS 6660 GB, NHMO.

Etymology: The species is named after the collector of the type Leif Aarvik (MNHO), well known Tortricidae specialist, in acknowledgment of his friendship.

Diagnosis: The three species described here are closely similar in wing pattern, but the forewing apex is more pointed, with termen oblique in *A. ustjuzhanini*, rounded with termen slightly oblique in *A. aarviki* and rounded with termen almost straight in *A. bernardlandryi*; the costa is almost straight in *A. bernardlandryi*, gently arched in *A. aarviki* and more definitely arched in *A. ustjuzhanini*; the white streak on the costa is shorter and intermediate in width in *A. aarviki*, narrower and almost reaching the base in *A. bernardlandryi* and wider and almost reaching the base in *A. ustjuzhanini*; the subterminal area is narrow with inner margin almost straight in *A. bernardlandryi*, slightly wider and with inner margin slightly concave in *A. aarviki,* and wider still with inner margin straight but oblique in *A. ustjuzhanini*. The hindwing is pale ivory yellow in *A. aarviki*, off-white with scattered brown suffusion and with terminal line brown in *A. bernardlandryi*, and pure white in *ustjuzhanini*.

The female genitalia are similar in the three species, but *A. aarviki* has the ninth abdominal segment moderately bulged dorsally, the ostium bursae large and the ductus bursae half sclerotized, as opposed to the papillae anales dorsally produced, the ninth abdominal segment moderately sclerotized dorsally, ostium bursae small and ductus bursae sclerotized only basally in *A. bernardlandryi*. *A. ustjuzhanini* has the ninth abdominal segment strongly bulged dorsally, the ostium bursae small and the ductus bursae sclerotized only basally.

Description (Fig. 3): Wingspan 28 mm. Labial palpus 3.5 x eye diameter, brown with upper and inner side white. Maxillary palpus basally brown, then white. Antenna brown, basally simple, distally lightly dentate. Frons rounded, produced, pale brown. Vertex white with brown line medially. Patagia white, dark brown laterally. Tegulae dark brown with thin outer border white. Thorax white. Forewing subrectangular, with rounded apex and termen almost straight; ground colour bronze brown sprinkled with black; costa shape basally bronze brown, then white sprinkled with black; dorsum white sprinkled with black; medial stripe white ending under cell; postmedial interveins silvery white; subterminal area reaching apex, white intensely sprinkled with black; terminal line brown; fringes bronze brown with medial line white; underside brown, off-white distally and with costa and dorsum white; terminal line brown; fringes white tipped bronze brown. Hindwing pale ivory yellow; fringes white; underside white with costa and veins suffused with brown. Legs bronze brown with inner side white; tibial spurs long and thin, the outer one shorter. Abdomen with first tergite bright white, second to forth bronze brown suffused with white, then white suffused with bronze brown; sternites white suffused with reddish brown; anal tuft yellow.

Female genitalia (Fig. 23). Papillae anales slightly concave, densely covered with setae; lower edge hardly traceable, fused with ninth abdominal segment. Ninth abdominal segment strongly sclerotized, bulged dorsally. Apophyses posteriores basally only recognizable by a comma-like sclerotization, ending shortly pointed close to apophyses anteriores. Abdominal segment VIII sclerotized. Apophyses anteriores as long as apophyses posteriores. Ostium bursae large, rounded, slightly produced. Ductus bursae 1.2 the length of corpus bursae, funnel-shaped for 2/3, then cylindrical. Ductus seminalis branching off at 2/3 of ductus bursae. Corpus bursae suboval, wrinkled.

Male unknown.

Biology: Unknown.

Distribution: Presently known from the Iringa Region in Southern Tanzania only.

Afroromieuxia bernardlandryi sp. n.

Figs 1, 2, 12, 14, 22

Material examined

Holotype: Male; [DRC], H[au]t Katanga, Tshinkolobwe, 10.xii.[19]30, J[ean] Romieux, GS 6903 GB, MHNG.

Paratypes: Male, same locality and collector as

Figs 21-23. Female genitalia. (21) *Diploschistis stygiocrena*, DRC. (22) *Afroromieuxia bernardlandryi*, paratype. (23) *A. aarviki*, holotype.

holotype, 18.xii.[19]30, RCGB. – Female, some locality and collector as holotype, 15.xii.[19]30, GS 6720 GB, MHNG. – Male; some locality and collector as holotype, 17.xii.[19]30, GS 2206 GB, MHNG. – Male; Elisabethville [DRC, Haut Katanga, now Lubumbashi], 8.XII.1937, Ch. Seydel [legit], GS 3223 GB, RMCA. – Female; Elisabethville, 28.x.1932, Ch. Seydel [legit], GS 6911 GB. RCGB.

Diagnosis: For differences from *A. aarviki* and *A. ustjuzhanini* externally and in the female genitalia, see the diagnosis under *A. aarviki*. In the male genitalia the feature of the uncus and gnathos associated with the strongly developed pars basalis of the valva, the dorsally produced vinculum and the two large subapical teeth in the phallus are unlike all known Afrotropical species of Ancylolomiini.

Etymology: The species is dedicated to Bernard Landry (MHNG), well known Crambinae specialist, a colleague, but above all a great friend over the last few decades.

Description (Figs 1, 2): Wingspan: holotype 26 mm; males 25 and 26 mm; females 28 and 29 mm. Labial palpus 4 x eye diameter, bronze brown bordered white; inner side white. Maxillary palpus basally bronze brown, apically white. Antenna biserrate in male, filiform in female, with scape white, then brown with bronze brown costa. Frons rounded, slightly produced, white. Vertex white. Patagia white with lateral edge dark brown. Tegulae dark brown with external border white. Thorax white. Forewing and hindwing as in Figs 1, 2 and under diagnosis of *A. aarviki*. Forewing fringes bright golden brown with double medial band white. Underside of forewing bright brown medially, suffused with white elsewhere and with terminal line brown; underside of hindwing brown along costa, then white and with terminal line light brown. Abdomen off-white with first three tergites suffused with brown; sternites more intensely suffused with brown. Legs bronze brown with inner side white; tibial spurs small, strongly asymmetrical, first pair longer than apical pair.

Male genitalia (Figs 12, 14). Uncus twice as long as tegumen, narrow, basally with round patch of spinulae, arched distally and pointed apically. Gnathos slightly shorter than uncus, subtriangular basally, then thin, upcurved and pointed. Tegumen short, triangular. Vinculum strongly produced dorsally, with lateral arms subrectangular. Juxta v-shaped with apical tips triangular. Pseudosaccus minute. Valva subrectangular, twice as long as uncus; basal costal process 0.8 as long as uncus, distally upcurved and wrinkled. Phallus subcylindrical, with two triangular, serrated apical teeth; vesica without cornuti.

Female genitalia (Fig. 22). Papillae anales strongly produced dorsally, fused with ninth abdominal segment. Ninth abdominal segment more sclerotized ventrally. Apophyses posteriores basally a hardly traceable line, then arched and with rounded tip. Abdominal segment VIII bulged dorsally and sclerotized medially. Apophyses anteriores 0.7 as long as apophyses posteriores, straight, with rounded tip. Ostium bursae rounded, sclerotized, slightly produced. Ductus bursae half the length of corpus bursae, wrinkled. Ductus seminalis branching off at 0.75 of ductus bursae. Corpus bursae broad, suboval, with two vertical stripes of spinulae.

Biology: Unknown.

Distribution: Presently known from the DRC, Haut-Katanga Province only.

Afroromieuxia ustjuzhanini sp. n.

Figs 4, 16, 20

Material examined

Holotype: Female; East Africa, Zambia, Northern Zambia Prov[ince], Mutinondo Wilderness, 12°27'S 31°17'E, 01.i.2011, Kovtunovich & Ustjuzhanin [legunt], GS 5330 GB, 58550 Collezione Bassi, RCGB.

Etymology: The species is named after one of its collectors, Petr Ustjuzhanin (Altai State University, Barnaul, Russia), well-known Pterophoridae and Alucitidae specialist, with many thanks for his friendship.

Diagnosis: For differences from *A. aarviki* and *A. bernardlandryi* externally and in the female genitalia, see the diagnosis under *A. aarviki*.

Description (Fig. 4): Wingspan 29 mm. Labial palpus 4 x eye diameter, bronze brown bordered white; inner side white. Maxillary palpus basally bronze brown, apically white. Antenna filiform, with scape white, then bronze brown. Frons rounded, slightly produced, off-white with edge bronze brown. Vertex white suffused with pale yellow laterally and with brown line medially. Patagia white with lateral edge dark brown. Tegulae dark brown with external border white. Thorax brown, off-white distally. Forewing and hindwing as in Fig. 4 and under diagnosis of *A. aarviki*. Forewing fringes bright silvery grey with medial band white. Underside of forewing brown medially, suffused with white elsewhere; underside of hindwing brown along costa, then white. Abdomen: first segment and anal tuft white, other segments off-white densely suffused with grey brown. Legs bronze brown with inner side white; tibial spurs small, asymmetrical, both pairs of same length.

Female genitalia (Fig. 20). Papillae anales produced ventrally, densely covered with setae; lower edge not traceable, fused with ninth abdominal segment. Ninth abdominal segment sclerotized, strongly bulged dorsally. Apophyses posteriores basally only recognizable by a comma-like sclerotization, ending shortly pointed close to bases of apophyses anteriores. Abdominal segment

VIII well developed, sclerotized. Apophyses anteriores short, as long as apophyses posteriores. Ostium bursae moderately enlarged, sclerotized, slightly produced. Ductus bursae half the length of corpus bursae, funnel-shaped for 2/3, then cylindrical. Ductus seminalis branching off at 2/3 of ductus bursae. Corpus bursae suboval, medially bulged, with a patch of spinulae medio-ventrally.

Male unknown.

Biology: Unknown. The holotype was attracted to artificial light in open mixed forest (Fig. 16).

Distribution: Presently known from Northern Zambia only.

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REFERENCES

Bassi G. 2013. Revisione delle specie afrotropicali del genere *Ancylolomia* Hübner, [1825]. I: i gruppi *indica* e *chrysargyria* (Lepidoptera: Pyralidae, Crambinae). *Shilap. Revista de Lepidopterologia, Madrid* 41(164): 517-529.

Bassi G., Trematerra P. 2014. The Crambinae from Ethiopia and Mozambique collected by the University of Molise expeditions in 2008 and 2009 (Lepidoptera: Pyraloidea: Crambidae, Crambinae). *Entomologia* 2: 35-45.

Błeszyński S. 1970. A revision of the oriental species of the genus *Ancylolomia* Hübner (Studies on the Crambinae, Lepidoptera, Pyralidae, Part 49). *Tijdschrift voor Entomologie* 113: 27-43.

Hampson G.F. 1898. On a collection of Heterocera made in the Transvaal. *Annals and Magazine of Natural History, including Zoology, Botany and Geology, London* (ser.7) 1: 158-164.

Hampson G.F. 1910. Zoological collections from Northern Rhodesia and adjacent territories: Lepidoptera Phalaenae. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London* 1910 (2): 388-10, pls 36-41.

Hampson G.F. 1919. Descriptions of new Pyralidae of the subfamilies Crambinae and Siginae. *Annals and Magazine of Natural History, including Zoology, Botany and Geology*, London (ser. 9) 4: 53-68, 137-154, 305-326.

Hübner J. 1796-1836 [imprint "1796"]. Sammlung europäischer Schmetterlinge. 8. Horde. Die Schaben; nach der Natur geordnet, beschrieben und vorgestellt. *Augsburg*. [1]-[12]-13-70-[71]-[78], pls 1-71.

Klots A.B. 1970. Lepidoptera. *In:* Tuxen SL (Ed.), *Taxonomist's glossary of genitalia in insects*. (Second revised and enlarged edition). *Munksgaard, Copenhagen*, pp. 115-130.

Kristensen N. P. 2003. Skeleton and muscles: adults. *In:* Kristensen N. P. (Ed.), Lepidoptera, moths and butterflies. Vol. 2. Morphology, physiology, and development. *Handbook of Zoology* IV (36): 39-131. *Walter de Gruyter, Berlin, New York.*

Landry B. 1995. A phylogenetic analysis of the major lineages of the Crambinae and of the genera of Crambini of North America (Lepidoptera: Pyralidae). *Memoirs on Entomology International, Gainesville* 1: 1-242.

Léger T., Landry B., Nuss M. 2019. Phylogeny, character evolution and tribal classification in Crambinae and Scopariinae (Lepidoptera, Crambidae). *Systematic Entomology* 44: 757-776.

Meyrick E. 1937. *Exotic Microlepidoptera. Taylor and Francis, London*, pp. 1-160.

Ragonot E.L. 1889. *In:* de Joannis J., Ragonot E.L. 1889. Descriptions de genres nouveaux et espèces nouvelles de Lépidoptères. *Annales de la Société Entomologique de France*, Paris (ser. 6) 8[3 (1888)]: 271-284, pl. 6.

Robinson G.S. 1976. The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologist's Gazette* 27: 127-132.

Swinhoe C. 1886. On the Lepidoptera of Bombay and the Deccan. Part IV. Heterocera (continued). *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London* 1885 (4): 852-886.

Tams W.H.T. 1932. New species of African Heterocera. *The Entomologist*, London 65 (829): 124-129, pl. 4.

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